

EVOLUTION OF THE FAGACEAE: THE IMPLICATIONS OF FOLIAR FEATURES¹

JAY H. JONES²

ABSTRACT

The leaf architecture and cuticular morphology of extant Fagaceae have been examined and compared to those of putatively fagaceous fossil forms. The various leaf types found among extant Fagaceae appear at different times in the fossil record. The most recent types to evolve are typical lobed oak forms (Oligocene-Miocene) whereas coarsely toothed oaks and regularly craspedodromous chestnut-like leaves are found as early as the Eocene. There are no leaf forms directly comparable to modern Fagaceae in pre-Eocene sediments but the presence of well defined vegetative and reproductive materials of two distinct modern subfamilies in the Eocene suggests that this family arose in or before the Paleocene. Leaf forms generally comparable to those of the Fagaceae do occur in the Paleocene. The characteristics of these early forms, especially those of the secondary venation and margin, suggest a common origin with the Betulaceae and reaffirm the close affinity of these two families. *Nothofagus* leaves are distinct from those of all other Fagaceae suggesting that this taxon should be considered a separate family as proposed by Kuprianova and Nixon on other grounds. Nothofagaceae also seem to be closely related to the Betulaceae and probably arose from the same fagalean stock. Suggestions that modern lobed oaks are atavistic expressions of primitive palmately lobed-compound forms, variously assigned to *Debeya*, *Dewalquea*, and *Araliopsis*, although possibly correct, are poorly supported by foliar data. Foliar features also fail to provide convincing support for the origin of the Fagaceae from Cretaceous platanoids.

The Fagaceae comprise a large and important family of trees and shrubs (Lawrence, 1951), yet we know little about their evolution. The fossil record of the family reportedly extends back to the Cretaceous (Berry, 1923) but pre-Tertiary records have been questioned in recent years (Wolfe, 1973). Nineteenth and early twentieth century reports are especially questionable because they usually were based on the superficial resemblance of fossil materials, most commonly leaves, with those of extant plants (Dilcher, 1973, 1974). Because any complete evolutionary study must include information from both fossil and modern organisms (Simpson, 1953; Wolfe, 1973), it is important to study fossil materials in sufficient detail to assure accurate taxonomic placement. This requires not only a detailed study of the fossil material but also a detailed knowledge of the nature and variation of the same characters in similar modern plants. Much work has been done on modern Fagaceae (Trelease, 1924; Camus, 1928–1929, 1934–1954; Brett, 1964; For-

man, 1966a; Elias, 1971; Soepadmo, 1972; and others), yet even Camus, in her monumental monographs of the chestnuts and oaks (1928–1929; 1934–1954), did not provide much of the information on foliar characteristics necessary for the proper interpretation of fossil leaves. A primary objective of the research upon which this paper is based (Jones, 1984) was to examine thoroughly the foliar characteristics of extant Fagaceae using modern methods of leaf architectural and cuticular analyses (Stace, 1965; Hickey, 1973, 1977, 1979; Dilcher, 1974; Hickey & Wolfe, 1975). Information obtained from this study (Jones, 1984) has provided a basis for the interpretation of putatively fagaceous fossil leaves as well as useful information for testing classification schemes of modern Fagaceae, which are based primarily on nonfoliar features.

The goal of this paper is to integrate newly acquired foliar information with other vegetative, reproductive, and fossil information in order to provide a view of the evolution of and

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² Indiana University, Bloomington, Indiana 47405. Present address: ARCO Resources Technology, 2300 West Plano Parkway, Plano, Texas 75075.

within the Fagaceae. Past taxonomic treatments of the Fagaceae are reviewed first, followed by a discussion of the classification and evolutionary history of each genus with emphasis on the contribution of foliar information. Discussion of reproductive aspects, although taken into consideration, has been kept to a minimum because these have been reviewed in great detail elsewhere (Hjelmqvist, 1948; Brett, 1964; Forman, 1964a, 1966a, 1966b; Soepadmo, 1968a, 1968b, 1970; Abbe, 1974; Fey & Endress, 1983; Kaul & Abbe, 1984). The final section of this paper provides an assessment of the contribution of foliar information to classification, primarily above the generic level, and to understanding of the origin and evolution of the family within the Amentiferae. Keys for confirming fagaceous affinities among hamamelidopsid leaf materials and generic affinities within the Fagaceae are found in Appendix I and Appendix II respectively. Illustrations and descriptions of trichome types found in this family are presented in Appendix III.

TAXONOMIC REVIEW OF THE FAGACEAE

The constituent genera of the Fagaceae have been surveyed in numerous works. From the time of Ray (1682, 1703) members of the genera *Quercus*, *Fagus*, and *Castanea* have been grouped with other amentiferous plants (Stern, 1973). De Jussieu (1789) formalized the concept of the Amentiferae and included the above genera in the "order" Amentaceae. Dumortier in 1829 was allegedly the first to recognize the family (Soepadmo, 1972), and de Candolle (1868) was the first to circumscribe the family in its present form. He applied the name Cupuliferae, which has been used since in numerous ways by various authors. Oersted (1871) subdivided the Cupuliferae, used here at the familial level, into three subfamilies along lines approximating those drawn by recent students of this family (e.g., Forman, 1966a). Bentham and Hooker (1880) treated the Cupuliferae as an "order" with three tribes. The circumscription of the tribe Quercineae conforms to that of the Fagaceae of modern authors. However, Bentham and Hooker did not subdivide this tribe further, above the generic level, and thus their scheme does not provide taxa corresponding to modern subfamilies. The name Fagaceae was first used by Prantl (1894), who absorbed the "subfamily" Quercineae, sensu Oersted, into the Castaneae and reduced the number of genera in the family from seven to

five. Brett (1964) retained Prantl's subfamilial classification but recognized, at least tacitly, nine genera. Schwarz (1936a) appears to be the most extreme "splitter" among western botanists. He recognized 11 genera distributed among the traditional three subfamilies. With the possible exception of Schwarz, modern treatments of the Fagaceae are remarkably uniform in spite of significant intrageneric variability and the remarkable similarity between some elements of different genera. The suprageneric classifications of Forman (1966a), Hutchinson (1967), and Elias (1971) are identical. Melchior's (1964) system differs in that the genus *Trigonobalanus* is placed in the Fagoideae rather than the Quercoideae. Lozano-C. et al. (1979), in a report of a third species of *Trigonobalanus*, established a fourth subfamily, the Trigonobalanoideae, to accommodate this problematic genus. Most recently Smiley and Huggins (1981) adopted Forman's (1966a) classification with the addition of the subfamily Pseudofagineae to house the fossil genus *Pseudofagus*. The analysis of another fossil form (Manchester & Crane, 1983), *Fagopsis*, presented an equally good case for the erection of a new subfamily if not a new family. However, none was proposed by the authors. The recognition of *Nothofagus* as a separate family, first proposed by Kuprianova (1962), also seems to be gaining support (Nixon, 1982), but no comprehensive scheme of classification containing this innovation has been published. A summary of the more important classification schemes, together with a proposed classification based on the integration of foliar information, is found in Table 1.

GENERIC ANALYSES

FAGUS L.

The genus *Fagus* exhibits very little morphological variation. This is not only true of leaves (Jones, 1984) but also extends to reproductive features (see, for example, Praglowski, 1982) and nonfoliar vegetative features such as wood (Shimaji, 1962). The homogeneity of this genus has apparently made it an unattractive candidate for monography. It is the only genus of Fagaceae for which there is no recent comprehensive monograph. The most complete recent works dealing with *Fagus* are the palynological studies of Hanks and Fairbrothers (1976) and Praglowski (1982). No formal subgeneric groups of *Fagus* species have been established in these or other works.

TABLE 1. Taxonomic treatment of fagaceous plants by various authors. Inclusions noted are relative to the classification of Forman (1966a) and others.

de Candolle 1868	
Family Cupuliferae	
<i>Fagus</i> (incl. some <i>Nothofagus</i>)	
<i>Nothofagus</i>	
<i>Castanea</i>	
<i>Castanopsis</i> (incl. <i>Chrysolepis</i>)	
<i>Quercus</i> (incl. <i>Lithocarpus</i>)	
Oersted 1871	
Family Cupuliferae	
Subfamily Fagineae	
<i>Fagus</i>	
<i>Nothofagus</i>	
Subfamily Castaninae	
<i>Castanea</i> (incl. <i>Castanopsis</i> & <i>Chrysolepis</i>)	
<i>Pasania</i>	
<i>Cyclobalanus</i> (incl. <i>Lithocarpus</i>)	
Subfamily Quercineae	
<i>Quercus</i>	
<i>Cyclobalanopsis</i>	
Prantl 1894	
Family Fagaceae	
“Subfamily” Fageae	
<i>Fagus</i>	
<i>Nothofagus</i>	
“Subfamily” Castaneae	
<i>Castanea</i> (incl. <i>Castanopsis</i> & <i>Chrysolepis</i>)	
<i>Pasania</i>	
<i>Quercus</i>	
Schwarz 1936a	
Family “Cupuliferae”	
Subfamily Fagoideae	
<i>Fagus</i>	
<i>Nothofagus</i>	
Subfamily Castaneoideae	
Tribe Castaneae	
<i>Castanea</i>	
<i>Castanopsis</i> (incl. <i>Chrysolepis</i>)	
Tribe Pasanieae	
<i>Pasania</i>	
<i>Cyclobalanus</i>	
<i>Lithocarpus</i>	
Subfamily Quercoideae	
Tribe Cyclobalanopsidae	
<i>Cyclobalanopsis</i>	
<i>Erythrobalanus</i>	
Tribe Querceae	
<i>Macrobalanus</i>	
<i>Quercus</i>	

TABLE 1. Continued.	
Brett 1964	
Family Fagaceae	
Subfamily Fagoideae	
<i>Fagus</i>	
<i>Nothofagus</i>	
Subfamily Castaneoideae	
Tribe Castaneae	
<i>Castanea</i>	
<i>Chrysolepis</i>	
<i>Castanopsis</i>	
Tribe Lithocarpeae	
<i>Lithocarpus</i>	
Tribe Pasanieae	
<i>Pasania</i>	
Tribe Querceae	
<i>Quercus</i>	
<i>Cyclobalanopsis</i>	
Melchior 1964	
Family Fagaceae	
Subfamily Fagoideae	
<i>Fagus</i>	
<i>Nothofagus</i>	
<i>Trigonobalanus</i>	
Subfamily Castaneoideae	
Tribe Castaneae	
<i>Castanea</i>	
<i>Castanopsis</i> (incl. <i>Chrysolepis</i>)	
Tribe Pasanieae	
<i>Pasania</i>	
<i>Lithocarpus</i>	
Subfamily Quercoideae	
<i>Quercus</i>	
Hutchinson 1967	
Elias 1971	
Family Fagaceae	
Subfamily Fagoideae	
<i>Fagus</i>	
<i>Nothofagus</i>	
Subfamily Castaneoideae	
<i>Castanea</i>	
<i>Castanopsis</i>	
<i>Chrysolepis</i>	
<i>Lithocarpus</i> (<i>Pasania</i>)	
Subfamily Quercoideae	
<i>Quercus</i>	
<i>Trigonobalanus</i>	
Soepadmo 1972	
Forman 1966a	
Family Fagaceae	
Subfamily Fagoideae	
<i>Fagus</i>	
<i>Nothofagus</i>	

TABLE 1. Continued.

Subfamily Castaneoideae
<i>Castanea</i>
<i>Castanopsis</i> (incl. <i>Chrysolepis</i>)
<i>Lithocarpus</i>
Subfamily Quercoideae
<i>Quercus</i>
<i>Trigonobalanus</i>
Lozano-C. et al. 1979
Family Fagaceae
Subfamily Fagoideae
<i>Fagus</i>
<i>Nothofagus</i>
Subfamily Castaneoideae
<i>Castanea</i>
<i>Castanopsis</i>
<i>Lithocarpus</i>
<i>Chrysolepis</i>
Subfamily Quercoideae
<i>Quercus</i>
Subfamily Trigonobalanoideae
<i>Trigonobalanus</i>
Smiley and Huggins 1981
Family Fagaceae
Subfamily Fagoideae
<i>Fagus</i>
<i>Nothofagus</i>
Subfamily Pseudofagineae
<i>Pseudofagus</i>
Subfamily Castaneoideae
<i>Castanea</i>
<i>Castanopsis</i>
<i>Lithocarpus</i>
Subfamily Quercoideae
<i>Quercus</i>
<i>Trigonobalanus</i>
Present Study
Family Nothofagaceae
<i>Nothofagus</i>
Family Fagaceae
Subfamily Fagoideae
<i>Fagus</i>
Subfamily Castaneoideae
<i>Castanea</i>
<i>Chrysolepis</i>
<i>Castanopsis</i>
<i>Lithocarpus</i>
Subfamily Trigonobalanoideae
<i>Trigonobalanus</i>
Subfamily Quercoideae
<i>Quercus</i>

Paleobotanists have made informal groupings based on relatively minor differences in leaf characteristics. Tralau (1962), for example, divided the beeches into *Fagus* ‘grandifolia’ and ‘sylvatica’ types in his investigation of fossil *Fagus* from Europe. Pollen data seem to at least partially support this distinction (see Praglowski, 1982). Tanai (1974) distinguished three groups based primarily on a leaf index (i.e., length/width × 100) and the number of secondary veins but again avoided the establishment of any formal infrageneric taxa. Tralau (1962) suggested that the ‘sylvatica’ and ‘longipetiolata’ groups intergrade and are best considered as one. If it were not for geographical separation this intergradation might apply to the ‘sylvatica’ and ‘grandifolia’ groups as well. In fact, Hanks and Fairbrothers (1976) found that none of the groups proposed by Tralau (1962) and Tanai (1974) clustered tightly on the basis of pollen features. The lack of formal subgeneric taxa, therefore, seems quite reasonable.

Foliar information confirms the relative uniformity within this genus and can be used only in a very limited fashion for classification below the generic level (as in Cooper & Mercer, 1977). The observed intraspecific variation in foliar characteristics often exceeds interspecific variation. There are no clear cut qualitative differences that can be used to distinguish subgroups. In contrast, foliar information is very useful for the recognition of *Fagus*, whose leaves can be distinguished from those of other amentiferous families as well as other genera of Fagaceae (Appendices I and II). The margin, secondary venation, intercellular ridge sinuosity of the upper cuticle, and rather restricted complement of trichome types (see Text-Fig. 1 and Appendix III) are the most characteristic features of these leaves (Jones, 1984).

The fossil record of *Fagus* was thought to extend far back into the Cretaceous (Berry, 1923). However, most reports of Cretaceous *Fagus* have been based on isolated leaves that are often poorly preserved and frequently bear only a superficial resemblance to those of *Fagus* (see Lesquereux, 1874). Some describe leaves that do not even resemble modern *Fagus*. Others describe leaves from sediments that have been shown to be much younger than originally thought. Wolfe (1973) suggested that there are no valid reports of any Fagaceae prior to the Paleocene. Muller (1981) suggested that the earliest reliable pollen record is that of *Fagus granulata* (Piel, 1971) from the Lower Oligocene of Canada. There are

	<i>Fagus</i>	<i>Nothofagus</i>				<i>Castanea</i>	<i>Chrysolepis</i>	<i>Castanopsis</i>	<i>Lithocarpus</i>	<i>Trigonobalanus</i>	<i>Quercus</i>						
											<i>Cyclobalanopsis</i>	<i>Cerris</i>	<i>Mesobalanus</i>	<i>Lepidobalanus</i>	<i>Macrobalanus</i>	<i>Protobalanus</i>	<i>Erythrobalanus</i>
		<i>I</i>	<i>II</i>	<i>III</i>	<i>IV</i>												
Unicellular																	
1. Solitary	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
2. Conical	•	•	•	•	•	•		•	•	•							
3. Papillae									•		•						
4. Appressed laterally attached											•						•
5. Fasciculate						•		•	•	•	• ¹	•	•	•	•	•	•
6. Stellate						•	•		•		• ¹	•	•	•		•	•
7. Fused Stellate									•		• ¹	•		•			
8. Stipitate fasciculate									•		• ¹	•	•	•			•
9. Appressed parallel tuft									•								
10. Multiradiate									•								•
Intermediate																	
11. “Thick”-walled peltate							•										
12. Curly thin-walled					•												
13. “Thin”-walled peltate								•	•								
14. Rosulate									•		• ¹	•					•
Glandular																	
15. Simple uniseriate	•					•			•	•	•	•	•	•	•	•	•
16. Capitate or irregularly multiseriate						•						•	•	•	•	•	•
17. Large globular		•	•	•													
18. Branched uniseriate								• ²	•	•		• ¹	•		•	•	
19. “Glandular” peltate										•							

TEXT-FIGURE 1. Distribution of trichome types within the Fagaceae. See Appendix III for thorough descriptions and illustrations of each type. ¹Not observed in this study but reported in Camus (1934–1954). ²Not observed in this study but reported in Camus (1928–1929).

reports of earlier occurrences that may be accurate but need to be studied further. For example, Krutzsch (1970) reported fagoid pollen from the Eocene of Europe, but provided neither detailed descriptions nor figures. Kedves (1967) also reported fagoid pollen from the Eocene of

Europe. Pollen with the general form of that from *Fagus* has been reported from late Cretaceous sediments (Srivastava, 1969; Jarzen & Norris, 1975) but Muller (1981) has rejected these as not representing *Fagus*. *Fagus*-like wood has been reported from the Upper Cretaceous of Japan

(Stopes & Fuji, 1910), the Lower Senonian of western Germany (Vater, 1884), and other European and North American localities. There is also one unconfirmed report of *Fagus* wood from South America (Salard, 1961). The first presumed fruits of *Fagus* appear to be those reported from the Middle–Upper Eocene “Wilcox” Flora of southeastern North America (Lesquereux, 1859). This report is based solely on gross external features and no subsequent reports of *Fagus* fruits have been made in spite of continuing work in the area. Brown (1944) considered a quadripartite structure, previously assigned to *Diospyros aspera* Berry, to be a *Fagus* cupule but Berry (1945) vigorously refuted the reassignment of this form. Brown (1944) also associated the fossil leaf form *Dryophyllum tennesseense* with the purported *Fagus* cupules. Upon reexamination, however, these leaves have been shown clearly not to be *Fagus* but rather a castaneoid type most likely associated with the genus *Castanea* (Jones, 1984). Thus, this report of Eocene *Fagus* is questionable. Manchester and Crane (1983) suggested that there are no confirmed reports of *Fagus* earlier than the Oligocene, yet, Takhtajan (1982) presented Eocene and even some Upper Paleocene records. There are certainly valid reports of this genus in the Oligocene (e.g., Conwentz, 1886; Chandler, 1957), and there are numerous reports of beech leaves and fruits in the Neogene (Unger, 1850; Kirchheimer, 1957; Tralau, 1962; Tanai, 1974; Van der Burgh, 1978a; Smiley & Huggins, 1981; Takhtajan, 1982). In summary, the fossil evidence currently available suggests that *Fagus* had evolved, certainly by the Oligocene, and perhaps as early as the Upper Paleocene.

The geographical distribution of *Fagus* ranges discontinuously over most temperate areas of the Northern Hemisphere. It is notably absent in some areas, such as western North America, where it is found only in the fossil record. There are no native *Fagus* in the Southern Hemisphere and reports of fossil *Fagus* from there are most likely in error. Many early reports result from the historical assignment of *Nothofagus* forms to the genus *Fagus* (see Ettingshausen, 1891). Others probably result from misidentifications based on superficial resemblances between *Fagus* and architecturally similar leaf forms such as *N. alessandrii*. In the Northern Hemisphere, *Fagus* appears to have been uniformly distributed over the major land masses with Neogene occurrences even in Alaska (Hollick, 1936) and Greenland

(Heer, 1883). The distribution of forms has undergone considerable contraction, particularly during the Pleistocene.

The origin of *Fagus* appears to have been in the Northern Hemisphere (Berry, 1923). Hanks and Fairbrothers (1976) placed the site of origin in south central Asia but Tanai (1974) reported older *Fagus* fossils from North America, implying a North American origin. Takhtajan's (1982) reports of Oligocene, Eocene, and Upper Paleocene *Fagus* in Asia, together with greater diversity, tend to support an Asian origin. In his 1969 treatise on the origin of flowering plants, Takhtajan in fact, explicitly suggested an east Asian origin for *Fagus*. Van Steenis (1971a) is more specific, asserting that the Fagoideae arose somewhere between Yunnan and Queensland with *Fagus* radiating from the Northern part of the region. Opponents (e.g., Schuster, 1972), have contended that the region circumscribed by van Steenis is not consistent with current geological interpretations, which suggest that this area was widely separated until the late Tertiary. Although van Steenis' hypothesis has largely been dismissed, the site of origin for *Fagus* is still a subject of debate.

A recent paper by Hickey et al. (1983) is particularly germane to the discussion of centers of origin. These authors suggested that, on the basis of new paleomagnetic data, the age assessments of many high latitude floras, modified in recent years on the basis of paleofloristic similarities with “younger” floras of lower latitudes, may be as old as originally thought. If their conclusions are accurate, many plants and terrestrial animals occur at high latitudes up to 18 million years before they occur at mid-latitudes. Although there has been much concern over some of the paleomagnetic and other interpretations made in this particular study (Kent et al., 1984; Norris & Miall, 1984; Hickey et al., 1984), the once popular belief that temperate floral elements differentiated at high latitudes may be valid for many species. It seems that *Fagus* fits this pattern very well. I find this hypothesis to be very appealing but a better knowledge of the fossil floras of southeast Asia as well as those of higher latitudes is needed to confirm or refute it.

Both Tralau (1962) and Tanai (1974) found *Fagus grandifolia*-like fossils antedating the *F. sylvatica* types. The *F. grandifolia*-like forms are also the most widely distributed, occurring in the fossil record of Europe, Asia, and North America until the end of the Tertiary. The *F. sylvatica* and

F. longipetiolata types have not been found outside Europe and Asia. At the end of the Tertiary the 'grandifolia' types became extinct in all but North America. Available paleobotanical data therefore, indicate that the 'grandifolia' type is primitive within the genus *Fagus*.

Foliar data, from extant plants, do not contribute much to the identification of a primitive form within the genus. The basic leaf architecture (i.e., characteristics of the margin, secondary veins, and gross form) of *F. grandifolia* approaches those of some species in the Castaneoideae and Quercoidae more closely than the 'sylvatica' or 'longipetiolata' types do, but such similarity in form is probably best explained by convergence rather than close proximity to a common ancestral form.

NOTHOFAGUS BLUME

Unlike *Fagus*, *Nothofagus* is not tightly bound together as a group on the basis of leaf characters. In fact, there are several different leaf types represented in this genus. The trichome complements are consistent, however, across most of the genus. None of the species bears tufts and nearly all are supplied with large, often resinous, globular to peltate trichomes. Short conical trichomes are also much more abundant in *Nothofagus* than in any genus of the Fagaceae sensu stricto. In spite of these common features, the leaf architecture is quite variable and few features characterize the genus as a whole. Because of this variability I differentiated four general leaf groups, each with a fairly distinct assemblage of characteristics that allows it to be distinguished from other groups of *Nothofagus* as well as other genera and families (Jones, 1984). The first (type I) can be briefly characterized as being evergreen and entire-margined. The second (type II) is evergreen with well developed serrations. The third (type III) is a rather heterogeneous group that is composed of deciduous nonentire-margined leaves. The fourth (type IV) is evergreen, entire-margined, and lacks the typical trichome complement characteristic of the above groups. A list of the species studied that belong in each group is given in Text-Figure 2.

The diversity and distribution of *Nothofagus* has made it an attractive subject for investigation (see, for example, Langdon, 1947; Camus, 1951; van Steenis, 1953, 1971a, 1971b; Cookson & Pike, 1955; Soepadmo, 1972; Hanks & Fairbrothers, 1976; Philipson & Philipson, 1979;

Romero, 1980; Ragonese, 1981; Humphries, 1981; Aguirre & Romero, 1982; Romero & Aguirre, 1982; Praglowski, 1982). The group has been variously subdivided on the basis of reproductive and vegetative features. The classification of van Steenis (1953) is generally accepted. This scheme is built, in part, on foliar features, and thus there is some correlation between it and the division by leaf types found in Jones (1984) (see Text-Fig. 2). Palynologists divide the genus into three groups based on pollen characteristics (i.e., 'menziesii,' 'fusca,' and 'brassi' types), but these too show considerable divergence from van Steenis's scheme. In the final analysis, *Nothofagus* appears to be a heterogeneous assemblage. There is little doubt they are all related, at least at the family level (see Nixon, 1982), but the affinities within this group are more obscure.

The intrageneric diversity is related to the phytogeographic distribution. Although restricted to the Southern Hemisphere, *Nothofagus* is fairly wide ranging with occurrences in temperate South America, Australia, Tasmania, and New Zealand as well as tropical New Britain, New Caledonia, and New Guinea. The tropical species form the most homogeneous and well defined group. This group collectively and exclusively possesses type I leaves with conduplicate vernation (Philipson & Philipson, 1979) as well as 'brassi' type pollen.³ Species of this type also possesses bipartite cupules, a character that can be found, only rarely, outside this group. In addition, the wood of these tropical forms appears to be consistent in form and distinguishable from those of temperate species (Dadswell & Ingle, 1954).

The temperate forms do not possess such uniformity even within "reproductively isolated" floral regions. For instance, the *Nothofagus* of South America, New Zealand, and Australia all possess more than one leaf type as well as multiple types of vernation and pollen (Text-Fig. 2). Both deciduous and evergreen forms can also be found in all but New Zealand. The distribution of these characteristics implies the existence of multiple parallel evolutionary events in several

³ Van Steenis (1971a) reported 'brassi' type pollen from *Nothofagus alessandrii*, a South American species that, according to Cranwell (1939), bears 'fusca' type pollen. Cranwell's assessment is probably correct. Praglowski (1982) as well as Hanks and Fairbrothers (1976) found 'brassi' pollen type to be exclusively associated with the tropical *Nothofagus* from New Guinea and New Caledonia.

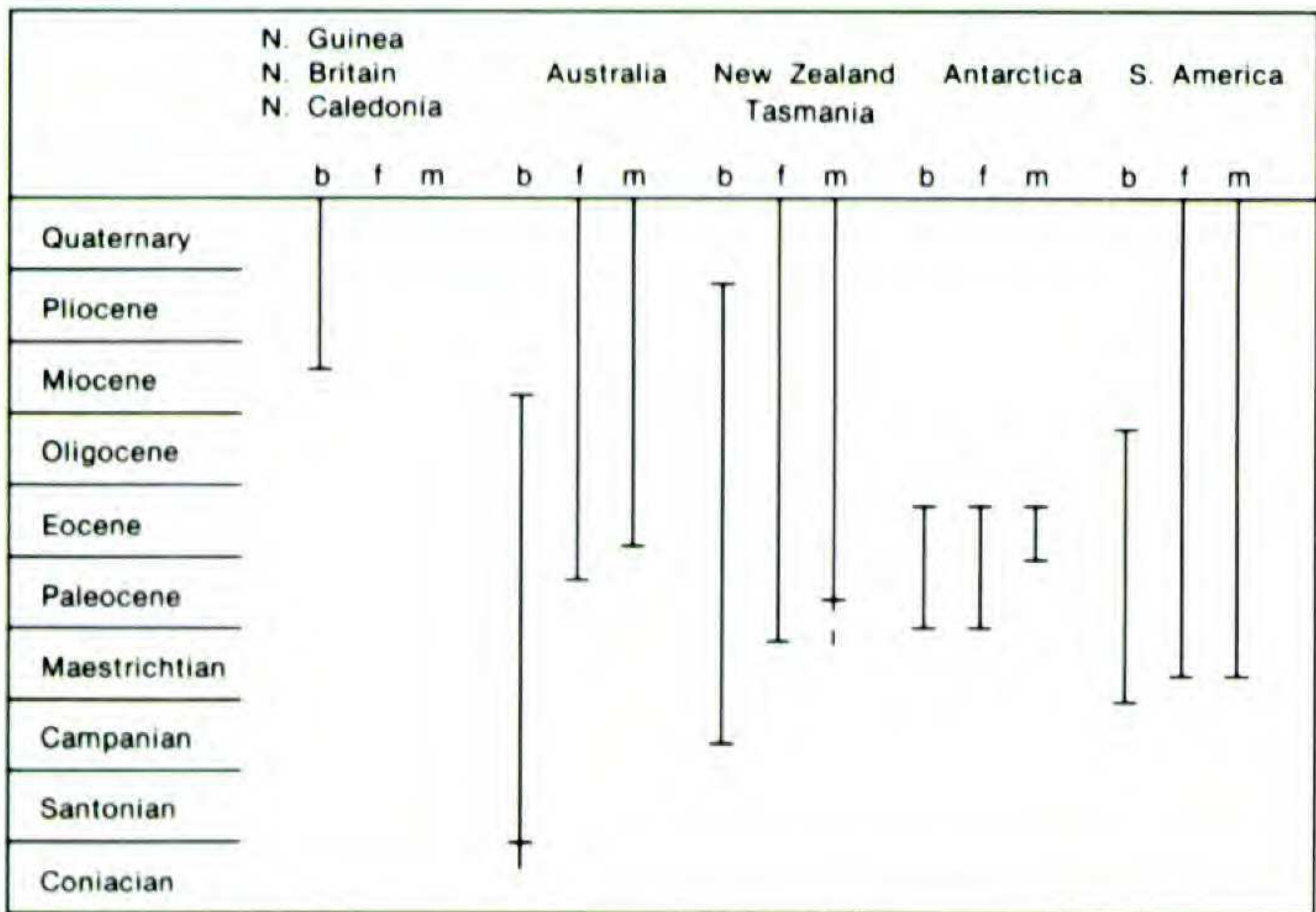
Species	van Steenis section	Subsection	Habit	Vernation	Pollen	# Cupule parts	Geographical distribution
Leaf type I							
<i>Nf. aequilateralis</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC ² (Trop.)
<i>Nf. balansae</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
<i>Nf. brassi</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG ² (Trop.)
<i>Nf. codonandra</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
<i>Nf. arenata</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
<i>Nf. discoidea</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
<i>Nf. grandis</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
<i>Nf. pullei</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
<i>Nf. rubra</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NC (Trop.)
<i>Nf. starkenborghi</i>	Calusparassus	Bipartite	e	Conduplicate	brassi	2	NG (Trop.)
Leaf type II							
<i>Nf. alessandri</i>	Nothofagus	Antarcticae	d	Plicate	fusca	2(4) ¹	SAm ² (Temp.)
<i>Nf. alpina</i>	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
<i>Nf. antarctica</i>	Nothofagus	Antarcticae	d	Plicate	fusca	4	SAm (Temp.)
<i>Nf. glauca</i>	Nothofagus	Antarcticae	d	Plicate		2(4) ¹	SAm (Temp.)
<i>Nf. gunnii</i>	Nothofagus	Antarcticae	d	Plicate	fusca	4	Tas ² (Temp.)
<i>Nf. obliqua</i>	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
<i>Nf. procera</i>	Nothofagus	Antarcticae	d	Plicate	menziesii	4	SAm (Temp.)
<i>Nf. pumilo</i>	Nothofagus	Pumiliae	d	Plicate	fusca	4(2) ¹	SAm (Temp.)
Leaf type III							
<i>Nf. betuloides</i>	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
<i>Nf. cunninghami</i>	Calusparassus	Quadripartite	e	Plane	menziesii	4	Aust ² (Temp.)
<i>Nf. dombeyi</i>	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
<i>Nf. fusca</i>	Calusparassus	Quadripartite	e	Revolute	fusca	4	NZ ² (Temp.)
<i>Nf. menziesii</i>	Calusparassus	Quadripartite	e	Plane	menziesii	4	NZ (Temp.)
<i>Nf. nitida</i>	Calusparassus	Quadripartite	e	Plane	fusca	4	SAm (Temp.)
<i>Nf. truncata</i>	Calusparassus	Quadripartite	e	Revolute	fusca	4	NZ (Temp.)
Leaf type IV							
<i>Nf. cliffortioides</i>	Calusparassus	Tripartite	e	Revolute	fusca	3	NZ (Temp.)
<i>Nf. solandri</i>	Calusparassus	Tripartite	e	Revolute	fusca	3	NZ (Temp.)

TEXT-FIGURE 2. Comparison of proposed classification, by leaf type, with that of van Steenis (as reported in Soepadmo, 1972) and some individual properties of *Nothofagus* species. ¹Disparant values for this variable exist for these species, those in parentheses are from van Steenis (1953) and the others are from Philipson and Philipson (1979). ²Aust = Australia, NC = New Caledonia, NG = New Guinea, NZ = New Zealand, SAm = South America, Tas = Tasmania.

character groups and/or the presence of the current diverse set of characters before reproductive isolation occurred (estimated by tectonic data to have been accomplished by the mid-Cretaceous; Smith and Briden, 1977).

Postulates based on plate tectonic information, such as that presented in Smith and Briden (1977), and biogeographic information do not conform to that from the fossil record. Tectonic data would indicate the existence of the ancestral group from which *Nothofagus* and other Fagaceae arose during the late Jurassic or early Cretaceous yet the earliest confirmed report of *Nothofagus* or any other Fagaceae does not occur until the Santonian (Muller, 1981) or perhaps Coniacian (Stover & Evans, 1973). This and all other Cretaceous reports of Fagaceae are based on pol-

len. The oldest record of *Nothofagus* (Dettmann & Playford, 1969) is from southern Australia. This pollen, *Nothofagidites senectus*, is of the 'brassi' type, which is the only type found until the middle to late Maestrichtian when the 'fusca' and 'menziesii' types appear simultaneously along with the 'brassi' type, in South America (Romero, 1973, 1977; Archangelsky & Romero, 1974; Menendez & Filice, 1975). The stratigraphic ranges of the pollen types in each major geographical region (Text-Fig. 3) imply a radiation of the 'brassi' type from southern Australia to South America and other points in its current range. The pollen record further suggests that the genus underwent considerable differentiation in or enroute to South America where the 'menziesii' and 'fusca' types first appear. These forms



TEXT-FIGURE 3. Distribution of *Nothofagus* pollen types (b = ‘brassi’; f = ‘fusca’; m = ‘menziesii’) through space and time; gaps are not shown. Modified and revised from Muller (1981) and Humphries (1981).

may have subsequently spread back across Antarctica to New Zealand and Australia. This hypothesis is highly conjectural at this point and must be tested along with a myriad of other hypotheses as we broaden the body of fossil evidence and determine, with greater accuracy, the stratigraphic position of previously reported forms. It should be noted that this and many other models require free routes of migration between South America and Australia at least into the Maestrichtian. Again, this is not in agreement with the current paleogeographic reconstructions. The cladistic representation of land mass separations constructed by Rosen (1978), however, indicates that sea boundaries were not formed until palynological differentiation, at least, had occurred. Van Steenis (1971a) circumvented discrepancies between the time of barrier formation and the emergence of various groups by suggesting the existence of some as yet unreported land bridges linking South America to Australia through Antarctica. Archipelagos or migrating microplates would account for the postulated migration. Schuster (1976) included reports of cordilleras that might satisfy van Steenis’s requirements. The strength of biological evidence for the existence of free paths for dispersal supports either the existence of these discontinuous pathways or the later estimates for the separation of the “*Nothofagus*” province. If the earlier estimates of separation are accurate and van Steenis’s land bridges did not exist, I would accept the occurrence of long distance transport, after the wide range of characters had evolved, rather than the multiple parallel evolutionary events that would be required to ex-

plain the current distribution of characters. Although unlikely, long distance dispersal may not be as irrational as it might first appear. It is true that an overwhelming body of evidence indicates that fruits of *Nothofagus*, and for that matter all extant Fagaceae, are not suited for long distance dispersal (Holloway, 1954; Cranwell, 1963, 1964; Preest, 1963). Yet, Tiffney (1984) has shown that substantial changes in fruit and seed sizes have occurred from mid-Cretaceous into the early Tertiary. The trends in size are undoubtedly correlated with changes in modes of dispersal and the evolution of various animal groups. Thus, the dispersal strategies exploited by fossil Fagaceae may have differed substantially from those of today. The presence of *Fagopsis*, a wind dispersed fagaceous plant from the Eocene and Oligocene of North America, underscores the need for flexibility when considering the dispersal mechanisms of fossil forms.

An intriguing phytogeographic problem is that of the center of origin and/or radiation. Postulated centers of origins include New Caledonia (Croizat, 1952), southeast Asia (Takhtajan, 1969), southeast Asia-Queensland (van Steenis, 1971a, 1971b), North America (Oliver, 1925; Schuster, 1976), Asia (Darlington, 1965), Northern Hemisphere (Raven & Axelrod, 1974) and “southern” (Couper, 1960a, 1960b; Cranwell, 1963). Although many postulate a northern origin, it is clear that most of the differentiation occurred in the Southern Hemisphere. A northern origin of *Nothofagus* (not a morphologically dissimilar ancestor) would likely leave a recognizable fossil record in that region. Although there have been several reports of *Nothofagus* or *Nothofagus* pollen from the Northern Hemisphere (Mtchedlishvili, 1961; Sein, 1961; Ames & Riegel, 1962; Kedves, 1964; Penny, 1969; Hopkins, 1969; Elsik, 1974), none provide convincing evidence for the existence of *Nothofagus* in that region. Pollen forms attributed to *Nothofagus* from the Maestrichtian of Siberia (Mtchedlishvili, 1961) and the Eocene London Clay (Sein, 1961) are said to be chloranthaceous (Kuprianova, 1967). She and others (e.g., Soepadmo, 1972) doubt the existence of *Nothofagus* in the Northern Hemisphere. Elsik (1974) refuted Kuprianova’s assessment on the basis of exine sculptural differences between the fossil forms she studied and extant Chloranthaceae. It is interesting to note, however, that the pollen Elsik assigned to *Nothofagus* has an exine sculpture that is quite distinct from all living members of this genus.

As he tangentially suggested, this form may represent a fagaceous or pre-fagaceous ancestral form since the sculpturing is more like that found in extant *Fagus* and *Quercus* than in *Nothofagus*.

Megafossil evidence of *Nothofagus* is also lacking in the Northern Hemisphere. Bandulska (1923, 1924) reported *Nothofagus* leaves from the Eocene of Bournemouth, but her description of the leaf architecture was very brief and did not contain any information to indicate that the specimens under consideration were actually *Nothofagus*. She admirably included information and an illustration of cuticle from these leaves but again the description was very brief and the illustration did not show any characteristics that would confirm the generic affinities of this leaf type. The T pieces or "dagger-like" structures of which she spoke are common to many fagaceous genera and their presence in cuticle preparations is often related to leaf age and the length of maceration during cuticle preparation. Complex gland bases, common to nearly all *Nothofagus*, were not mentioned in the description and were not evident in the illustration. No subsequent reports confirming or augmenting her report have been made. There are other leaves from the Northern Hemisphere with architecture similar to those of *Nothofagus*. *Phyllites kryshstofovichii* (Klimova) Iljinskaja et Ablaeu, for instance, has been compared to *Nothofagus moorei* (Takhtajan, 1982). No information on the cuticles of leaves such as these is available. Leaves of other members of the Hamamelidopsidae also possess the architectural characteristics of this and other similar leaf types, so until cuticular evidence is produced they cannot be considered as an indication of the presence of this genus in the Northern Hemisphere. There are no reports of wood, flowers, fruits, or other plant parts attributable to this genus from the Northern Hemisphere. A northern origin, for fully differentiated *Nothofagus*, therefore is unlikely. Raven and Axelrod's (1974) postulate that *Nothofagus* must have migrated to the Austral regions through Africa lacks corroborative fossil evidence. Raven and Axelrod (1974) recognized this deficiency, citing only two reports, one of which was attributed to contaminated drilling mud (Puri, 1965) and the other to windblown contaminants from South America (Schalke, 1973). Fossil evidence therefore strongly supports a southern origin for recognizable *Nothofagus*. This is not to say that a remote hamamelidopsid ancestor did not develop in the Northern Hemisphere and migrate to

the south via Africa as suggested by Raven and Axelrod (1974) or North America as proposed by Oliver (1925).

The fossil record of *Nothofagus* is well represented in the Southern Hemisphere (e.g., Couper, 1953, 1960a, 1960b; Cookson, 1958; Cranwell, 1959, 1963; Romero, 1973; and many others). Pollen has been extensively studied and is found in the remnants of Gondwanaland except India, disregarding one questionable report from the Miocene (Ramanujam, 1966), and Africa (Axelrod & Raven, 1978). These two land masses were the first to become isolated during the fragmentation of Gondwanaland. Axelrod and Raven (1978) suggested that the evergreen southern beech-podocarp forests must have extended into southern Africa, but again they conceded that there is no fossil evidence to corroborate this assumption. Surely pollen evidence would have been found if this were the case. *Nothofagus* is known to produce massive amounts of pollen (van Steenis, 1971a; Soepadmo, 1972) and it often occurs as a dominant element in fossil assemblages. To me the absence of fossil forms on these continents argues for an origin in the Austral complex after the separation of these two land masses.

Megafossils are also abundant, yet they have been largely neglected. Fossil wood (*Nothofagoxylon* Gothan) has been described from the Upper Cretaceous or Tertiary (age uncertain) of Antarctica (Gothan, 1908) and the Oligocene to Miocene of southern South America (Kräusel, 1924; Cozzo, 1950; Boureau & Salard, 1960; Salard, 1961; Ragonese, 1977). The wood described is all of temperate type. Leaves are very abundant (Berry, 1938; Menendez, 1971) and have been described from Antarctica (Dusén, 1908; Orlando, 1964; Zastawniak, 1981), Australia (Ettingshausen, 1888), New Zealand (Ettingshausen, 1887a; Oliver, 1936), Tasmania (Hill, 1983a, 1983b), and South America (Dusén, 1899–1902; Frenguelli, 1941). Many of the leaf types described in the early literature were assigned to *Fagus* in accordance with the plant classification schemes for modern Fagaceae in vogue at that time. Although some leaf types do not appear to be *Nothofagus* or any other Fagaceae, most are comparable with *Nothofagus* on the basis of the information available. Except for Hill (1983a, 1983b), none of the studies provide cuticular information.

Considering the abundance of the leaf record and the early and widespread occurrence of the

'brassi' type pollen, one might expect to find entire-margined evergreen (type I) leaves in the fossil record, but this is not the case. Yet, the apparent absence of these leaves may be due to difficulties involved in identifying entire-margined leaves rather than a true absence. Cuticular material, when available, is a great asset when working with nondescript entire-margined leaves. Close examination of austral fossil floras may well reveal the presence of these *Nothofagus* forms.

All fossil *Nothofagus* leaf materials reported thus far have been from the Tertiary. The accuracy and precision of the age determinations are poor in most cases. Thus, at present, the leaf record can tell us little more than that deciduous and/or evergreen temperate (types II and III) *Nothofagus* were present in South America, Antarctica, New Zealand, and Australia during the Tertiary. A comprehensive review of fossil *Nothofagus* leaf forms is desperately needed.

The leaf architectural and cuticular morphology of extant *Nothofagus* has been the subject of several recent papers. Romero and co-workers (Romero, 1980; Aguirre & Romero, 1982; Romero & Aguirre, 1982) have surveyed the leaf architecture of nearly the entire genus, providing keys for the identification of leaves to the species level. Bandulska (1924) surveyed the cuticle of some *Nothofagus* and *Fagus* species, but her analysis was limited to only a few species and employed a restricted set of characters. Ragonese (1981), however, provided a much more complete analysis in her anatomical assessment of *Nothofagus* leaves, but she investigated only the South American forms. The results of Jones (1984) are in general agreement with those of the above studies.

Little can be said about intrageneric evolution on the basis of extant leaf characteristics alone. Romero (1980) stated that *Nothofagus antarctica* leaves were the most primitive among those of the South American species but did not provide foliar evidence to support this assertion. It seems he was echoing the assertions of van Steenis and others based on the presence of "primitive" reproductive features such as a two-parted cupule. Type IV leaves, characteristic of *N. solandri* and *N. truncata*, are specialized and do appear to be advanced. They possess a rather unique trichome complement that lacks large glands, common in the rest of the genus, and possess a dense cover of curly, thin-walled, solitary trichomes on the abaxial surface. This trichome type is restricted

to this group with the exception of *Nothofagus glauca*, in which they are much less abundant and occur with thick-walled solitary trichomes and large glands. *Nothofagus gunnii* of Tasmania also lacks glands and possesses a rather distinct leaf architecture. This species may also represent a specialized form, but without corroborative fossil evidence we cannot know for sure. The often distinctive leaf architecture and rather unique cuticular characteristics should be of great value in the assessment of fossil *Nothofagus* leaf forms. The analysis of these forms will provide much valuable information about the evolutionary history of this important group particularly with regard to its origin and relationship to the Fagaceae sensu stricto and the Betulaceae.

CASTANEA MILL.

Castanea is a small genus of about 12 species, restricted to temperate regions of the Northern Hemisphere. It is a relatively homogeneous group showing little variability in leaf architecture and cuticular morphology. Reproductive and non-foliar vegetative features (see, for example, Shimaji, 1962) also exhibit little variation in this genus. Unlike *Fagus*, however, this genus has been studied fairly thoroughly. Camus (1928–1929) presented a thorough monograph of the genus in which she adopted the subgeneric classification proposed by Dode (1908). According to this scheme, *Castanea* is divided into three sections, *Eucastanon*, *Balanocastanon*, and *Hypocastanon*, mainly on the basis of reproductive features (i.e., those of the fruit and cupule). Foliar characteristics provide some support for this classification. The leaves of section *Eucastanon*, for example, generally have more prominent teeth with distinct bristle tips. The uniseriate (type 15) and capitate (type 16) trichomes also have less prominent basal cells in species of this section. Capitate trichomes with multicellular heads are abundant in section *Eucastanon* whereas simple uniseriates are more abundant in the other two sections. The monotypic section *Hypocastanon* can be roughly distinguished from the other sections by the lack of abundant trichomes and subtle teeth, which often lack bristles. Some specimens of *C. henryi*, in fact, possess upturned setaceous tips. None of these features, however, can be relied upon to clearly differentiate subsections. The intraspecific variation, once again, meets or exceeds that between most species. Graves (unpubl. data) faced this problem in his

attempt to construct a key to the species of *Castanea* based on foliar features. He emphasized the variability of the foliar features and stressed the importance of relying on a number of characteristics rather than one or only a few. In the final analysis he was unable to construct a key to the species based entirely on foliar features. The variability is probably due, at least in part, to the reproductive properties of the group. Facile formation of hybrids is one of the salient characteristics of the Fagaceae, and *Castanea* is no exception. The formation of natural hybrids has long been noted and has caused the taxonomy, particularly of the “chinkapin” species, to be quite unsettled.

Castanea species are discontinuously distributed in temperate regions of the Northern Hemisphere. This group does not appear to compete as favorably in the cooler parts of the North temperate zone as *Fagus*, *Quercus*, and many other elements of the temperate forests. Fossil records indicate a typical “holarctic” distribution with records from Greenland (Heer, 1883), Alaska (Hollick, 1936), western North America (LaMotte, 1952), and other regions in which *Castanea* is no longer found. Since there is undisputed proof of the existence of *Castanea* (i.e., inflorescences, cupules, pollen, and leaves) by the Eocene (Crepet & Daghljan, 1980; Jones, 1984), the current distribution is in harmony with plate tectonic evidence.

Reports of castaneoid fossils span from the Santonian to the present. The first records are in the form of pollen. Castaneoid (Tricolpollenites type) pollen has been reported from the Lower Campanian of the Netherlands as well as the Santonian/Campanian of western Canada (Rouse et al., 1971). *Cupuliferites pusillus*, another taxon associated with the Castaneoideae, has been reported from the Maestrichtian of California (Chmura, 1973). Pollen corresponding to this type was later reported from Eocene *Castanea* inflorescences from southeastern North America (Crepet & Daghljan, 1980). Castaneoid pollen has been reported from the Upper Paleocene (Gruas-Cavagnetto, 1978) and Lower Eocene (Kedves, 1978) of Europe as well. Reports from the Eocene to the present abound (Muller, 1981). Palynological data alone cannot be used to indicate the presence of *Castanea* but rather only the Castaneoideae.

Wood resembling that of *Castanea* (i.e., *Castanoxylon* Navale) has been reported from the Neogene of Europe and Eocene-Miocene of India

(Navale, 1964; Selmeier, 1970c; van der Burgh, 1978b). Wood, like pollen, is not generically specific in this group and similar wood is present in *Castanopsis* as well as some species of *Quercus* and *Lithocarpus* (Navale, 1964). *Castanea* flowers, which provide definitive proof, have been reported by Conwentz (1886) in the Eocene-Oligocene Baltic Amber and by Crepet and Daghljan (1980) from the Eocene of southeastern North America. There are very few reports of *Castanea* fruits in the fossil record. Kirchheimer (1957) listed only one doubtful occurrence (Beyn, 1940). Cupules have been found in the Eocene of southeastern North America (Crepet & Daghljan, 1980; Jones, 1984) but the only report of actual fruits is one of aborted fruits from the Pliocene of Germany (van der Burgh, 1978a). The rarity of *Castanea* as well as *Quercus* fruits in the fossil record is probably related to the lack of hard, durable ovary walls, or parts thereof, and the presence of abundant substrate for decomposer organisms. That the Pliocene fruits mentioned above were aborted fruits is consistent with this hypothesis. Most of the reproductive structures that were once assigned to *Castanea* are now considered to be *Castanopsis* (Kirchheimer, 1957), which is commonly reported from the Neogene of Europe.

The basic *Castanea* leaf form first appears during the Eocene in the form of *Dryophyllum tennesseense* (Jones, 1984). Similar leaves can be found in the Paleocene (e.g., Laurent, 1912; Crane, 1978), but few possess the regularity of secondaries and teeth characteristic of *Castanea* leaves, and those that do lack cuticle needed for identification. Many “castaneoid” leaf forms have been reported from the Eocene to the present (e.g., Nathorst, 1888; Berry, 1916; Knobloch, 1969; Takhtajan, 1982; Hummel, 1983). None of these leaves has been unquestionably associated with definitive reproductive materials, however, and similar forms can be found in other fagaceous and nonfagaceous genera. Many workers (e.g., Laurent & Marty, 1909; Ferguson, 1971) have specifically mentioned the difficulties involved when working with isolated *Castanea*-like leaves. The *Castanea*-like *Dryophyllum furcinervis* (Rossm.) Schmalh., for example, is thought by some to be *Castanopsis* (Kräusel & Weyland, 1950), whereas others hold it to be a distinct ancestral type (Raniecka-Bobrowska, 1962). Mai (1970) believed that the morphological and anatomical features are consistent with those of the genus *Trigonobalanus*. He further

suggested that these leaves are stratigraphically correlated with fossil fruits of this genus. Ferguson (1971) chose to leave it in the genus *Quercus* as suggested by Heer. Realistically, this leaf type could belong to this or to one of many other extant genera to which it has been assigned. It could just as easily represent an extinct form whether ancestral or not.

The foliar features of *Castanea* species do not provide any hint as to possible primitive forms within the genus. It may be possible to infer the primitiveness on the basis of correlated fruit and other features but even this would be tenuous when one considers the relative plasticity of leaf characters and the interspecific mixes characteristic of this taxon.

CHRYSOLEPIS HELMQV.

Chrysolepis consists of two sympatric species native to the Pacific western United States. This genus is recognized by many, but not all, prominent students of the Fagaceae (Hjelmqvist, 1948; Hutchinson, 1967; Forman, 1966b; Elias, 1971; Abbe, 1974). Others, Soepadmo (1972) for example, do not feel that the *Chrysolepis* species are sufficiently distinct to warrant separation from *Castanopsis*. In a communication to van Steenis, Soepadmo allegedly stated that if *Chrysolepis* is recognized as a separate genus at least one species from southeast Asia would have to be included (van Steenis, 1971a). Lawrence (1951) and Melchior (1964) did not recognize this genus but failed to support their position. Brett (1964) evidently did not recognize *Chrysolepis*, which is not too surprising since he also favored the fusion of *Castanopsis* and *Lithocarpus*, thus reducing the Castaneoideae to two genera.

Separation of *Chrysolepis* from *Castanopsis* is based primarily on differences in cupule structure (Forman, 1966b). Most of the other reproductive and vegetative features are similar if not identical. Erdtman (1943) for example, found the pollen of *Chrysolepis* (*Castanopsis*) *chrysophylla* to be indistinguishable from that of *Castanopsis* and *Castanea*. This has been supported recently using scanning electron microscopy (Crepet & Daghljan, 1980). The leaves of *Chrysolepis* and *Castanopsis* species are also very similar in gross form, venation, and cuticular characteristics. There are some differences, however, that can be employed to support the generic distinction. *Chrysolepis* leaves are generally smaller and somewhat xerophytically modified. Most tend to

be elliptical to oblong rather than lanceolate as in most *Castanopsis*. The most consistent difference is in the trichome complement. Even these are similar, but both species of *Chrysolepis* possess thick-walled peltate trichomes with radially aligned cap cells (type 11, see Appendix III), which are totally lacking in *Castanopsis* species. Similar peltate trichomes are found in other Castaneoideae (i.e., *Castanopsis* and *Lithocarpus*) but these trichomes (type 13) have very thin collapsible cell walls, and the cap is composed of nonradially aligned cells. The taxonomic significance of these differences can be debated, but they do allow one to distinguish *Chrysolepis* leaves from those of other genera. I believe *Chrysolepis*, although very closely related to *Castanopsis*, should be recognized at the generic level.

The phytogeography of *Chrysolepis* can be interpreted in two different ways depending on the basic assumptions made about the group. Neither of these can be confirmed or rejected with the data currently available. If the genus is an ancestral form not derived from or closely associated with *Castanopsis*, as suggested by Elias (1971), it simply has a very restricted relict distribution. Yet, if *Chrysolepis* species are closely allied derived forms, perhaps even congeneric with those of *Castanopsis*, which are restricted today to southeast Asia and surrounding islands, the disjunction must be explained by one or more of the following: 1) long distance dispersal, 2) a widespread ("holarctic") past distribution, and 3) plate tectonic anomalies (i.e., rafting on microplates). Long distance dispersal is generally ruled out because of the current dispersal strategies adopted by this and other groups of extant Fagaceae. In contrast, the fossil record indicates that the range of *Castanopsis* was indeed much greater in the past. There have been reports of *Castanopsis* in western North America, Asia, and Europe (Kräusel & Weyland, 1950; LaMotte, 1952; Kirchheimer, 1957; Takhtajan, 1982). If these reports are accurate they, collectively, indicate a near pan north temperate distribution for *Castanopsis*. The absence of reports from eastern North America and other portions of the north temperate zone may be more a function of biases in the identification of fossil leaves than true distributional gaps. Leaves, which are the bases for most of the reports, are mostly entire-margined in *Castanopsis*. They are difficult if not impossible to distinguish from a host of other entire- and nearly entire-margined forms on the basis of leaf architecture alone. Thus, when ana-

lyzing leaves using only leaf form and architecture, one could quite likely assign *Castanopsis* leaves to other taxa with similar leaves particularly when encountered in regions where *Castanopsis* leaves are not expected. One only has to examine the synonymy lists in LaMotte (1952) to recognize the taxonomic diversity of forms that resemble *Castanopsis*. Cuticular features are very valuable in distinguishing forms with similar leaf architecture, yet, they are often neglected even when cuticle is preserved. Regardless of whether or not these gaps in the distribution are filled, the reports that exist indicate a sufficiently wide distribution of *Castanopsis* to account for the presence of *Chrysolepis* in its present range.

Although the current distribution is easily explained on the basis of paleoenvironmental information and the movement of large continental plates, some workers have suggested that western North American–southeast Asian disjuncts may have arisen by rafting on microplates such as those that form the southern portions of Alaska. Such explanations need not be invoked in this case, and little evidence for rafting has been presented.

The fossil record of *Chrysolepis* is scanty. Since the pollen of all Castaneoideae are similar, the earliest records may range back to the Santonian–Campanian (Muller, 1981). Reports from California (Chmura, 1973) and western Canada (Rouse et al., 1971) indicate castaneoid pollen was present in and near the current range of *Chrysolepis* by the late Cretaceous. *Chrysolepis* leaves (*Castanopsis chrysophylloides* Lesq.) have been reported from the Eocene to Pliocene (LaMotte, 1952). Dorf (1938) reported a leaf form, which he believed was most closely related to *Chrysolepis* (*Castanopsis*) *sempervirens*, but this report, like all other reports of species assigned to this genus, is based on gross form and architecture alone. Some of these reports, particularly those of Upper Miocene and Pliocene forms, are reasonable, yet cupules, upon which definitive identification must rest, have not been found. Because of uncertainty in generic identification it is impossible to tell, with the information available, precisely when *Chrysolepis* first evolved. If, as Elias (1971) suggested, this is an ancestral form, we might expect it to have evolved very early in the history of the family. It might account, at least in part, for the early reports of castaneoid pollen. However, if it is an advanced offshoot of *Castanopsis* (Brett, 1964) that evolved independently only after geological and environ-

mental factors created reproductive isolation would we expect a post-Eocene, probably late Oligocene or early Miocene, origin. At present both an early origin, that is, Upper Cretaceous or Paleogene, and a late origin, that is, Neogene, seem equally plausible.

CASTANOPSIS (D. DON) SPACH.

Castanopsis is a fairly large genus estimated to contain from “approximately 30 species or more” (Hutchinson, 1967; Abbe, 1974) to about 120 species (Camus, 1928–1929; Forman, 1966b; Willis, 1973). The actual number of species is probably around 100, extrapolating from recent revisions (Soepadmo, 1972) of the Malaysian species. The lower estimates appear to come from nineteenth century works and/or the works of Soepadmo on Malaysian *Castanopsis*. The great variation in the estimated size of this genus is, in part, an indication that few have studied *Castanopsis* in its entirety. The only modern comprehensive treatment of the genus is that of Camus (1928–1929). Soepadmo (1968a, 1972) provided a more up to date treatment, but it is restricted to the Malaysian species and is not nearly as thorough as that of Camus. There are numerous, less comprehensive assessments included in papers dealing with the systematics of the Fagaceae in general, but these do not contain much information on foliar features.

Oersted (1871) and Camus (1928–1929) divided *Castanopsis* species into groups. Oersted (1871) absorbed the species of *Castanopsis* into *Castanea*, segregating them into three groups on the basis of foliar and reproductive features. Two groups were placed in the subgenus *Castanopsis*, within which he placed *Castanopsis* (*Castanea*) *indica* A. DC. ex Seem., a species with acute serrate leaves, in one section and those species with entire or paucidentate leaves in a second. The remainder of the *Castanopsis* species were segregated in a second subgenus, *Callaeocarpus* (Miq.) Oersted. De Candolle (1868) separated the species of *Castanopsis* in a similar fashion but held this genus to be distinct from *Castanea*. Camus (1928–1929) divided the species of this genus into three sections using only reproductive features. Unfortunately, there are no foliar features that can be used to clearly distinguish these three sections.

The degree of variation in the leaf architectural and cuticular features of *Castanopsis* leaves varies considerably. The margins, for example, range

from entire to completely serrate. The venation varies similarly from camptodromous to craspedodromous. The fine venation is fairly consistent within the group except as modified by gross architectural differences. There is some variability in the cuticle as well but nearly all have a rather distinct speckled appearance. The serrate forms tend to possess tufts (type 5 trichomes, see Appendix III), which are otherwise rare in this genus. Nearly all species possess thin-walled peltate to "stellate" (type 13) trichomes abundantly distributed over the lower epidermis. These trichomes often cover the lower surface and obscure other epidermal features. It is the bases of these trichomes that give *Castanopsis* cuticles their characteristic speckled appearance. This trichome type allows one to distinguish *Castanopsis* leaves from most other tropical fagaceous leaves. It does occur in a few *Lithocarpus* species though, making absolute determinations of these leaves impossible at the generic level. Similar trichome forms occur in *Trigonobalanus doichangensis* (type 19) and *Chrysolepis* (type 11), but these can be distinguished readily from those of *Castanopsis*.

In spite of the variability in foliar features within the entire genus, most species of *Castanopsis* bear leaves of a single general type. The basic form of these leaves is similar to those of mesic tropical species in other fagaceous genera. The abundance of this generalized leaf type in *Castanopsis* is probably due, in part, to the rather limited geographic distribution of this genus.

Castanopsis is native only in southeast Asia, Indonesia, Korea, and Japan but the phytogeographic distribution is reputed to have been much wider in the past (Soepadmo, 1972). Kirchheimer (1957) suggested that fruits assigned to *Castanopsis salinarum* (Unger) Kirchheimer from the Oligocene of Europe are definitively *Castanopsis*. Many others have reported *Castanopsis* fruits, leaves, and/or wood from the middle to late Tertiary of Europe (e.g., Notzold, 1961; Szafer, 1961; Raniecka-Babrowska, 1962; Mai, 1964; Selmeier, 1970a, 1970b, 1972; Jung et al., 1971; van der Burgh, 1973). Ogura (1949) has reported wood of this genus from Japan, and Takhtajan (1982) included a number of *Castanopsis* leaf forms from eastern Europe and Asia. Wolfe (1968) reported a new species of *Castanopsis* from the Eocene of North America and further suggested (1973) that leaf material (i.e., that of MacGinitie, 1941) is truly *Castanopsis* (non *Chrysolepis* Hjelm.). Dorf (1938) reported a *Cas-*

tanea-like form, which he believed to be *Castanopsis* sensu stricto from the Tertiary of Idaho. *Chrysolepis* forms are also present in western North America (Axelrod, 1944; Chaney, 1944). Yet, these North American reports, those in Takhtajan (1982), and most others dealing with leaf material fail to give any information on the cuticle of the fossils in question. Even with cuticle, the leaves of this genus are often indistinguishable from some species of *Lithocarpus* and *Quercus* (see for instance Forman, 1964a, 1966a, 1966b). Therefore, fossil forms cannot be assigned at the generic level with certainty. Kräusel and Weyland (1950) were the first to use cuticular features to classify material as *Castanopsis*, but few have utilized these important features since. There are no reports of fossil *Castanopsis* fruits, or other reproductive macrofossils, in either North America or Asia to corroborate questionable leaf data.

There are no credible megafossil records of *Castanopsis* prior to the Eocene. Yet, pollen comparable to that of *Castanopsis* has been reported as early as the Upper Cretaceous (Santonian/Campanian of Canada; Rouse et al., 1971). *Castanopsis*-like pollen has also been reported from the Eocene of Great Britain (Chandler, 1964) and Europe (Kedves, 1978). Reports of *Castanopsis*-like pollen are, in fact, quite common throughout the Northern Hemisphere since the Eocene (Muller, 1981). As previously mentioned, however, the pollen of *Castanopsis* is not distinct but rather belongs to a generalized "castaneoid" type. Therefore, the presence of this pollen type does not necessarily indicate the presence of *Castanopsis*.

The fossil record can be interpreted as indicating an origin perhaps as early as the Upper Cretaceous but more likely in the early Tertiary. This genus was apparently widely distributed during the Eocene to Miocene and was lost in North America, Europe, and most of Asia during the Pliocene. Modern phylogenies suggest a fairly long evolutionary history for this genus, but forms included by the modern circumscription of *Castanopsis* are not generally considered to be primitive within the family.

The foliar features of this genus do not appear to be particularly advanced or primitive. The peltate (type 13) trichomes seem, intuitively, to be somewhat advanced yet the speckled appearance, lent by the bases of these trichomes, is present in some early forms of *Dryophyllum* and similar leaf types (Jones, 1984). Although the

foliar characteristics do not tell us much about the evolutionary status of this group within the family, they do support the separation of *Castanea* from *Castanopsis*, instead of the union suggested by Oersted (1871) and Brett (1964). In addition to morphological differences indicated by other authors (e.g., Camus, 1928–1929; Forman, 1964a, 1966a, 1966b), *Castanea* species do not possess the peltate trichomes characteristic of *Castanopsis* but rather bear capitate trichomes and tufts that are rare or absent in extant *Castanopsis*.

LITHOCARPUS BLUME

Lithocarpus is a large complex genus estimated, by some, to contain about 300 species (Willis, 1973). It has been split into two or more genera by several investigators (Oersted, 1871; Schwarz, 1936a; Nakai, 1939; Masamune & Tomiya, 1948; Brett, 1964). Others have distributed "*Lithocarpus*" species among sections of the genus *Quercus* (de Candolle, 1868). Camus (1934–1954), Forman (1964a, 1964b), and Soepadmo (1970, 1972) suggested that there was no basis for splitting this taxon. The boundaries between *Lithocarpus*, *Castanopsis*, and *Quercus* have long been a subject of controversy. Modern workers agree that *Quercus* and *Lithocarpus* are phylogenetically distinct, even though they show many parallel traits (Brett, 1964; Forman, 1964a, 1966a; Soepadmo, 1970, 1972). Luong (1965) and Forman (1966b) further suggested that *Castanopsis* and *Lithocarpus* can be clearly separated, at least phylogenetically, using specific vegetative and reproductive features. It is clear, however, that considerable mosaic and parallel evolution has occurred in this family.

There is little correlation between foliar features and most intrageneric classification schemes, which are based primarily on cupule morphology and other reproductive features. For example, very few of Camus' 14 subgenera are distinct and homogeneous with respect to foliar features. *Lithocarpus* leaves, in general, show relatively little variability. They are usually entire or only partly toothed. Only *L. densiflorus* has strongly serrate margins and then only in a few forms (e.g., *L. densiflorus* forma *attenuato-dentatus*, Tucker et al., 1969). Leaves of *Lithocarpus* are persistent to tardily deciduous. The basic leaf form is, in fact, very similar to those of other tropical fagaceous genera (i.e., *Castanopsis* and *Quercus* particularly those of the subgenus *Cy-*

clobalanopsis). Fortunately, most leaves of this genus can be distinguished from those of other genera using epidermal features. Appressed laterally attached (type 9, see Appendix III) trichomes are present in nearly all *Lithocarpus* species, and it is interesting to note that recent revisions (Soepadmo, 1970, 1972) involve the transfer of many species lacking this trichome type to *Castanopsis* and *Quercus*. As the taxonomy of *Lithocarpus* is further refined, this character may approach perfect agreement with those that are definitive.

The relative uniformity of *Lithocarpus* foliar features is probably a function of its rather limited distribution. With the exception of *L. densiflorus*, this genus is restricted to southeast Asia, Indonesia, and southern Japan. *Lithocarpus densiflorus*, which is found only in the Pacific southwestern part of North America, has rather distinctive foliar characteristics. Leaves of this species lack acuminate tips as well as other features common to the tropical oriental species of this genus. These sclerophyllous leaves invariably lack the appressed laterally attached (type 9) trichomes, common to most *Lithocarpus* species, and possess unique multiradiate (type 10) trichomes. The differences between the leaves of this species and those of the eastern species suggest rather distant affinities. Forman (1964a, 1964b, 1966a, 1966b; pers. comm., 1980) and others (e.g., Soepadmo, 1972) indicated, however, that the reproductive and nonfoliar vegetative features clearly associate this species with *Lithocarpus*. Although *L. densiflorus* may fit within *Lithocarpus*, the disparity in the foliar characteristics suggests a significant period of reproductive isolation in dissimilar environments.

The presence of *Lithocarpus* on both sides of the Pacific Ocean implies that this genus had a more extensive range in the past that must have bridged Asia and North America. Thus fossil *Lithocarpus* might be expected to occur at high northern latitudes on both continents. One might also assume that the distribution would extend to Europe as well since this is a pattern common to many contemporary floral elements. Yet, reports of this genus from the Northern Hemisphere are extremely rare. LaMotte (1952) listed only one North American species, *L. klamathensis* (MacGinitie) Axelrod, which occurs in the Miocene and Pliocene of the Pacific Northwest. Axelrod (1966) subsequently reported *Lithocarpus* leaves and a cupule from the Eocene (age uncertain) of Nevada. Axelrod and Raven

(1978) suggested that Miocene *Lithocarpus* gave rise to forms of *L. densiflorus* that occur in California today. Cuticular information, currently unavailable, should help to clarify the affinities of these fossil leaves.

Reports are equally rare from Europe. Saporta and Marion (1878) established the genus *Pasaniopsis* to contain *Pasania* (*Lithocarpus*)-like fossil leaves from the Paleocene Gelinden Flora. Only leaf architectural information is given for this material. It is consistent with placement near *Lithocarpus*, but cuticular information is needed before this leaf type can be allied to this genus with confidence. Andreánsky (1966) reported "undoubted" *Lithocarpus* from the Oligocene of Hungary. Yet, the published description and figures do not reveal a basis for this assignment. Only two probable fossil *Lithocarpus* species have been reported from Asia (Takhtajan, 1982). These two leaf forms are from Kazakhstan, and their ages were not reported. The figures of these leaf types reveal intersecondary veins and biconcave teeth that are not characteristic of *Lithocarpus* leaves. It is unlikely that these leaf forms belong to this genus.

The pollen of *Lithocarpus*, as previously mentioned, is of a generalized type and cannot be distinguished from other castaneoidean forms. Records of this pollen type, however, are common throughout the Northern Hemisphere. The first records of this type of pollen are from the Upper Cretaceous (Santonian/Campanian) of Canada (Rouse et al., 1971). No additional reports of wood, fruits, flowers, or other fossil materials have been made.

The paucity of fossil *Lithocarpus* in present North Temperate zones may be a function of difficulties in the identification of isolated organs of this genus rather than a true absence. MacGinitie (1969) acknowledged these difficulties when describing a leaf form from the Eocene Green River Flora. He contended, however, that suitable distinctions could be made in most cases if fourth order venation was available. Unfortunately, he did not mention the specific characteristics with which these distinctions can be made. I did not observe any reliable differences in the higher order venation of these genera.

Foliar features generally confirm the integrity of the genus as it has been recently circumscribed (Camus, 1934–1954; modified by Soepadmo, 1970, 1972). However, they do support the distinction of *Limlia* as suggested by Masamune and Tomiya (1948) on other grounds. The fea-

tures upon which this genus was originally based seem rather weak and when considered alone would not, in my opinion, justify separation at the generic level. However, *Limlia* leaves are distinct from those of nearly all *Lithocarpus* in that they lack type 9 trichomes and possess a dense coat of type 13 trichomes as in *Castanopsis*. Interestingly, additional work on wood anatomy (Lee, 1968) has shown that the closest affinities of the species in question lie with *Castanea* and *Castanopsis* rather than *Lithocarpus*. This is consistent with the aforementioned leaf data. Hence, the recognition of this somewhat intermediate taxon at the generic level may be warranted. The same epidermal characteristics support the retention of the *Castanopsis fissa*-group in *Castanopsis* rather than inclusion in *Lithocarpus* as suggested by Camus (1934–1954).

Finally, the significance of the foliar features of *Lithocarpus densiflorus* deserves consideration. The presence of a unique trichome complement and distinctive leaf architecture sets this species apart from all other *Lithocarpus*. Foliar features would provide very strong support for generic distinction if other, more definitive, features so indicated. The intraspecific variability in foliar characteristics would also support recognition of some varieties as separate species (e.g., *L. densiflorus* var. *echinoides*).

TRIGONOBALANUS FORMAN

The genus *Trigonobalanus* was established in 1962 by Forman with a complement of one species, *T. verticillata*, and was expanded to two species, with the reassignment of *Q. doichangensis* Camus, in Forman's detailed description of the genus (1964a). Lozano-C. et al. (1979) further expanded the genus to three species as the result of the discovery of *T. excelsa* in South America. The small size and proposed primitive position of this taxon (see Forman, 1964a) has made it an attractive subject for investigation (see Forman, 1962, 1964a, 1966a; Cutler, 1964; Erdtman, 1967; Forman & Cutler, 1967; Hou, 1971; Soepadmo, 1972; Lozano-C. et al., 1979; Menega, 1980; Hernández-Comacho et al., 1980; Baas, 1982). This genus has been assigned to various subfamilies (Forman, 1964a, 1964b; Melchior, 1964; Lozano-C. et al., 1979) but has not been formally subdivided above the species level. *Trigonobalanus*, small as it may be, does show considerable intrageneric variation. Erdtman (1967) for example, felt that the pollen mor-

phology of *T. doichangensis* and *T. verticillata* differed sufficiently that inclusion in separate sections or even separate genera should be considered. Mennega (1980) found substantial differences between the wood anatomy of these two species as well but felt that they were congeneric and closest to the Quercoideae. The male inflorescences of *Trigonobalanus* species vary as well, ranging from rigid, as in the Castaneoideae, to flexuous, as in most Quercoideae.

The leaves of *Trigonobalanus* also exhibit major differences. *Trigonobalanus verticillata*, for example, possesses whorled leaves, a characteristic unique to this species within the Fagaceae. The leaves of all *Trigonobalanus* species are similar in form to those of many other tropical Fagaceae (i.e., some *Castanopsis*, *Lithocarpus*, and *Quercus*). All species possess entire or mostly entire leaves of similar gross form. *Trigonobalanus doichangensis*, however, has leaves that are distinct from the other two species in that they are invariably entire and possess cuticles bearing papillae and rather exotic multicellular "peltate" (type 19) trichomes. Baas (1982) correctly concluded that *T. doichangensis* is an outlier with respect to leaf anatomy. In fact, the leaves of *T. excelsa* (of South America) and *T. verticillata* (of Malaysia) share many more common foliar features than either do with *T. doichangensis* (of Thailand). In spite of substantial intrageneric variability, leaf architectural and cuticular features together still allow leaves of *Trigonobalanus* species to be distinguished from other tropical Fagaceae (see Appendix II).

The intrageneric variability is undoubtedly related to the wide "disjunct" distribution of this taxon. *Trigonobalanus* is found in Thailand, the Malay Peninsula, Borneo, Celebes, and in Colombia, South America. These ranges may well be extended in the future since the genus is so new and many of the areas in which it might likely be found are poorly explored. The known range of this genus is quite wide but patchy, suggesting it is a relict of a much broader past distribution. A once broad distribution is almost demanded in order to account for the present occurrences. The range of *Quercus*, although more extensive today, is quite similar to that of *Trigonobalanus*. Both were probably circumboreal in the past. *Trigonobalanus* probably entered South America during the Miocene along with *Quercus*. Neither genus has penetrated past Colombia in South America. Unlike *Quercus*, *Trigonobalanus* seems to have become extinct in

temperate regions, perhaps due to intolerance of the late Tertiary climatic deterioration. We must turn to the fossil record to confirm the presence or absence of this genus in higher latitudes of the Northern Hemisphere.

The fossil record of *Trigonobalanus* is very scanty. There are no confirmed reports of fossil *Trigonobalanus* pollen although it is very similar to that of *Quercus* and therefore may have been assigned to typical quercoid form genera. No *Trigonobalanus* wood, flowers, or fruits have been confirmed but paleogene reproductive materials under investigation by W. L. Crepet and S. R. Manchester may prove to be from plants of this genus. In addition, Forman (1964b) has suggested that the fossil fruits assigned to *Fagus succinea* Goeppert & Menge are quite similar to those of this genus. Mai (1970) assigned four fruit types from the Eocene and Miocene of Europe to *Trigonobalanus*. Forman (pers. comm., 1980) suggested that some of the types probably represent *Fagus* and others, although possibly *Trigonobalanus*, cannot be assigned to this genus with certainty using available information. Mai (1970) also suggested that these fruits were correlated with *Castanea*-like leaves previously assigned to *Dryophyllum furcinervis* Schmalhaus. The leaves have been placed in several genera including *Phyllites*, *Castanea*, *Quercus*, and *Castanopsis* (Kräusel & Weyland, 1950). The cuticle, as illustrated by Kräusel and Weyland (1950), indicates that the leaves probably do not represent *Castanea*. The trichome bases are scattered and simple, resembling those of *Castanopsis*. Mai (1970) correctly suggested that the epidermis is also similar to that of *T. doichangensis*. Yet, the leaf architecture is much more similar to extant members of the Castaneoideae than to those of extant *Trigonobalanus*. The nature of the trichomes themselves, when known, will probably shed some light on the affinities of this leaf type. The reports of *Trigonobalanus* (Mai, 1970; Gregor, 1980; Takhtajan, 1982), if correct, would support the hypothesis of a Laurasian distribution during the Tertiary. We still do not have any significant indication that *Trigonobalanus* was present in North America. A search for this genus in the fossil record of this continent is in order.

Trigonobalanus must have evolved prior to the Eocene (most likely in the latest Cretaceous or Paleocene) if it is an ancestral form within the Quercoideae (see Forman, 1964a, 1966a; Elias, 1971). If *Trigonobalanus* evolved from a casta-

neoid ancestor, as Forman (1966a) and Elias (1971) imply on the basis of cupule characteristics, and if the cupule characteristics are linked to foliar characteristics, we might assume that leaves of the most primitive *Trigonobalanus* would most closely resemble those of the supposed ancestors (i.e., near *Chrysolepis*, Elias, 1971). If these assumptions are correct, *Trigonobalanus doichangensis* would be the most primitive species in this genus. This species possesses entire leaves and multicellular branched trichomes that sometimes resemble the scales of *Castanopsis*. This hardly seems to be the case however, since this species is more advanced with regard to reproductive features that are usually considered to be more conservative (i.e., flexible male catkins and cupules usually bearing a single fruit). However, the scale-like trichomes may be derived, as they appear to be based on trichome data alone. We must remember that the evolutionary rates and even directions of various organs and characters can differ. Thus, primitive foliar characters cannot be determined with certainty using information gathered from extant species alone. It seems advisable to wait for further information on the nature of fossil forms before making firm conclusions about evolutionary trends in leaf characteristics of this group.

QUERCUS L.

Quercus is the largest genus in the Fagaceae, with an estimated 300 (Lawrence, 1951; Elias, 1971) to 600 (Soepadmo, 1972) species. This genus has been studied often, but, because of its immense size and wide distribution, few have studied the genus in its entirety. Camus (1934–1954) has comprehensively monographed the genus in three monumental volumes. Although some disagree with finer points of her classification scheme, most modern taxonomists generally accept Camus' circumscription of the genus. Historically, however, the circumscription of the genus has been highly controversial. Some have suggested that it is heterogeneous enough that it should be divided into two or more genera. Schottky (1912), Hjelmqvist (1948), Brett (1964), and others, for example, recognized Camus' subgenus *Cyclobalanopsis*, as a separate genus. Schwarz (1936a) went so far as to divide *Quercus* into four separate genera. A significant number of taxonomists accept the recognition of *Cyclobalanopsis* (e.g., Hsu & Jen, 1979) but few support the extensive splitting proposed by Schwarz

(see, for example, Muller, 1942a). In contrast, many have suggested that *Quercus* should be united with morphologically similar *Lithocarpus* (e.g., de Candolle, 1868; Bentham & Hooker, 1880; Corner, 1939). Most modern workers (e.g., Camus, 1934–1954; Forman, 1964a, 1966a; Melchior, 1964; Soepadmo, 1968b, 1972) have suggested that there is a clear basis for distinguishing these as two genera. This certainly seems to be the case from a palynological point of view, but the intrageneric variability and extensive parallelism in wood, leaves, fruits, and other features often make discrimination difficult without detailed examination of fertile material.

Foliar variation in *Quercus* is not tightly correlated with established major infrageneric classification. Leaves of the subgenus *Cyclobalanopsis* (sensu Camus, 1934–1954) can be separated from those of the subgenus *Euquercus*, but there is considerable overlap among the sections of the latter. The sections often can be differentiated in a particular geographical area (Trelease, 1924; Dyal, 1936; Muller, 1942b; Barnett, 1944), but the distinctions become obscure when species from other geographical areas are considered. Numerous examples of parallel and convergent evolution of leaf forms have been noted in this genus (Tucker, 1974). Foliar variation in *Quercus* seems to be more closely associated with phytogeographic and environmental factors than with the definitive reproductive features that are the basis for classification at the section level.

Quercus has the widest distribution of all fagaceous genera. Its species are found in nearly all north temperate forests and woodlands, often as dominant elements. They are also abundant in subtropical and tropical regions of the Northern Hemisphere extending into the Southern Hemisphere only in northern South America and Indonesia. The wide geographical distribution probably accounts, at least in part, for the large variation in leaf form observed within *Quercus*. Brenner (1902) noted correlations between many foliar features and the geographical origin of the specimens. He also experimentally demonstrated substantial intraspecific effects of the environment on leaf form.

There is more foliar variability in this genus than in any other genus of Fagaceae. The leaves range from entire, nearly glabrous, tropical forms with drip tips and a coriaceous texture, to lobed, hairy, chartaceous forms characteristic of many temperate species. Camus (1934–1954) and others have noted the existence of specific leaf types

among *Quercus* species. There are entire-margined “laurel” and “willow” oaks, spiny sclerophyllous “holly” oaks, chartaceous “chestnut” oaks as well as typical lobed “white” and “red” oaks. Unfortunately, the types are not section specific, making classification at this level difficult when using leaf material alone (see Text-Fig. 4). Even trichome complements fail to allow clean separation of sections. This foliar variability often extends to lower taxonomic levels. The foliar variation within species is frequently dramatic, and foliar characteristics of species sometimes intergrade. Such intergradation is often the result of actual gene flow between species. The oaks are noted for their propensity toward hybridization (Trelease, 1917; Muller, 1942a, 1942b, 1952; Stebbins et al., 1947; Palmer, 1948; Bray, 1960; Benson, 1962; Hardin, 1975; Jensen & Eshbaugh, 1976), calling into question strict application of the biological species concept (Muller, 1942a; Burger, 1975; Crovello, 1976; van Valen, 1976). The capacity for genetic exchange may be one of the factors that makes the oaks very competitive in a wide range of environments.

The present broad distribution of *Quercus* is in harmony with the fossil record of this group. *Quercus*, like most fagaceous genera, had a “holarctic” distribution during the Neogene. There are abundant reports of fagaceous fossils from North America (see Trelease, 1918, 1924; LaMotte, 1952). These include reports of leaves (e.g., Lesquereux, 1878; Edwards, 1931; Chaney & Sanborn, 1933; Axelrod, 1956, 1964; Dorf, 1960, 1964; MacGinitie, 1969; Daghljan & Crepet, 1983; Manchester, 1983), wood (e.g., Platen, 1908; Schuster, 1908; Eames, 1910; Boeshore & Jump, 1938; Beyer, 1954; Prakash & Barghoorn, 1961a, 1961b; Wheeler et al., 1978), and reproductive materials including inflorescences (e.g., Daghljan & Crepet, 1983), nuts (e.g., Newberry, 1898; Manchester, 1981a, 1983), and cupules (e.g., Bones, 1979; Daghljan & Crepet, 1983; Manchester, 1983). *Quercus* remains are also abundant in Europe (Andreánsky & Kovacs-Sonkody, 1955; Kirchheimer, 1957). Leaves are reported most often (e.g., Schimper, 1870–1872; Kovacs, 1961; Andreánsky, 1966; Gazeau & Koeniguer, 1968; Sitar, 1974; Petrescu, 1976; Gros, 1983; Hummel, 1983), fruits (e.g., Heer, 1869; Saporta & Marion, 1878; Raniecka-Bobrowska, 1962; Hummel, 1983), cupules (e.g., Goeppert, 1855; Gregor, 1980; Hummel, 1983), and wood (Müller-Stoll & Madel, 1957; Brett, 1960; Selmeier, 1971; Prive, 1975), are also very

General leaf type	Cyclobalanopsis	Euquercus					
		Cerris	Mesobalanus	Lepidobalanus	Macrobalanus	Protobalanus	Erythrobalanus
Entire or partially toothed, elliptical to lanceolate evergreen	•			•		•	•
Entire, broad broadly deciduous to evergreen				•			•
Xeromorphic, sclerophyllous, small, entire margined evergreen		•		•		•	
Sclerophyllous holly-like		•		•	•	•	•
Craspedodromous "chestnut"-like	(•)	•		•	•		(•)
Rounded coarsely toothed, deciduous			•				•
Roundly lobed deciduous		•	•	•			•
Sharply lobed deciduous		•		•			•

TEXT-FIGURE 4. Distribution of general leaf types among the subgenera and sections of *Quercus*.

common. Takhtajan (1982) listed and illustrated many *Quercus* leaves, woods, and reproductive materials from eastern Europe and Asia. Hu and Chaney (1940) reported *Quercus*-like leaves of the castaneoid type from the Oligocene to the Pliocene of China. More recent Chinese reports (Chinese Neogene Plant Editorial Group, 1978; Shuangxing, 1980) listed several fagaceous fossils including *Quercus* leaves from the Eocene. A large amount of work has been done on the Tertiary flora of Japan, and many species of *Quercus* and other fagaceous genera have been found (Nathorst, 1888; Tanai & Onoe, 1961; Chaney, 1963; Tanai & Suzuki, 1965; Matsuo, 1968; Tanai, 1970; Tanai & Yokoyama, 1975). *Quercus* has been reported also from various arctic and other high latitude localities (Heer, 1870, 1883; Hollick, 1936; Koch, 1963). It appears that *Quercus* is a recent immigrant to Africa for it is found only near the Mediterranean from the late Neogene to the present (Kräusel, 1939; Raven & Axelrod, 1974). There have also been reports from Australia and other Southern Hemisphere localities, beyond the current range (Ettingshausen, 1887a, 1887b, 1888; Krasser, 1903; Berry, 1923), but these appear to be in error. The fossil record of *Quercus* parallels that of many other north temperate arborescent forms. *Quercus* appears to have been an important part of the “Arcto-Tertiary” geoflora. During the course of the Tertiary, species of this group have migrated latitudinally in response to climatic conditions (see, for example, Tanai, 1961, 1967; Tanai & Huzioka,

1967), but they have maintained their ability to compete favorably with other broad-leaved forms. Unlike *Lithocarpus* and *Castanopsis*, *Quercus* has survived in Europe as well as Asia and across North America.

The time and place of the origin of *Quercus* is uncertain. Pollen of the *Quercus* type has not been found in sediments older than the Oligocene (Muller, 1981). Yet, many reports of Cretaceous leaves exist (e.g., *Quercophyllum chin-kapinense*, Ward, 1905, Cenomanian). Most are poorly preserved and none have proven to be *Quercus*. Trelease (1918, 1924), although accepting the presence of *Quercus* in the Cretaceous, noted that many fossil leaves assigned to this genus are placed there for lack of a better place to put them. This is particularly true of the fossil leaf types he assigned to form groups that have no counterparts among modern *Quercus* (e.g., *Fraxinifolae*, *Distinctae*, and *Suspectae*). The tendency to assign fossil leaves to *Quercus* without solid morphological or anatomical evidence is probably a function of two intrinsic properties of the oaks. First, they are so widespread and abundant that oaks might be expected in almost any Northern Hemispheric arborescent angiosperm flora. Second, *Quercus* leaves are so variable that counterparts to many fossil leaf forms can be found among the highly variable and wide ranging leaf types found among modern members of this genus. The first believable, but still not conclusive, record of *Quercus* (Bones, 1979; Manchester, 1981a, 1983) is from the Middle Eocene Clarno Formation of Oregon. Leaves and wood, as well as nuts and cupules can be found here, strongly suggesting the presence of *Quercus* in fairly modern form at that time. Floral elements are needed to confirm the generic affinity, however, since the features found in the fossils are not definitive. Similar wood and fruits can be found, for example, in *Lithocarpus*. Crepet and Zavada (1983) have an inflorescence that is essentially like those of *Quercus* from the Middle Eocene Claiborne Formation (possibly Upper Paleocene–Lower Eocene Wilcox Formation; Zavada, pers. comm.) of Tennessee. The pollen, however, is different from that of typical *Quercus* pollen. The significance of the differences are currently being evaluated and may be developmentally rather than taxonomically related. It is likely that this will prove to be the earliest definitive evidence for the existence of *Quercus* or a close relative thereof. Flowers of this genus have been reported from the Eocene-Oligocene

Catahoula Formation (Daghlian & Crepet, 1983). Based on this evidence we can say that *Quercus* was definitely present by the Oligocene and was probably present in the Eocene or perhaps earlier.

When the leaf record is examined, we find that the earliest apparently valid reports of *Quercus* are of entire- and serrate-margined forms. Brenner (1902) felt that the entire-margined forms were indeed the most primitive within the genus. There are lobed forms reported from the Cretaceous, but the nature of the leaves themselves does not provide convincing evidence of fagaceous affinity. In fact, they are most often closer to other extant families. The first plausible lobed oak is that reported by Daghlian and Crepet (1983) from the Oligocene. Lobed forms do not become common, however, until the Miocene (Tanai & Yokoyama, 1975). Ruffle and Knappe (1977) suggested that lobation in oaks is an atavistic phenomenon that recalls the palmately lobed nature of distant ancestors, presumably of the *Debeya-Dewalquea* complex (see also Ruffle, 1978, 1980). This is an interesting hypothesis, but there does not seem to be much evidence to support it at this time. Holly-like *Quercus* leaves have been reported from the Cretaceous and throughout the Tertiary. Ettingshausen (1896) felt that this was the primitive leaf form within the genus and that all other forms were derived. This is a common form in the section *Protobalanus*, which is held to be primitive among American oaks. Trelease (1918, 1924) believed that all the American oaks evolved from a single holly oak ancestor (i.e., a mid-Tertiary *Q. chrysolepis*-like form). A few of the early holly oak fossils may well be ancestral within *Quercus*, yet, some have been shown to belong to *Ilex* or *Nyssa* when examined more closely (Kvaček & Walther, 1981). This leaf type became common during the Miocene, when drier climates, for which this leaf type is best suited, prevailed.

Castanea-like leaves are also among the oldest to be assigned to *Quercus*. However, forms with regularly spaced, uniform teeth and secondaries do not appear until the Eocene. These “chestnut” forms may be *Quercus*, but leaves of this type are very difficult to distinguish from similar forms in other genera of Fagaceae as well as some non-fagaceous taxa. The problems of determining the generic affinities of these forms have been discussed by numerous authors (e.g., Trelease, 1924; Schwarz, 1936b; Camus, 1934–1954; MacGinitie, 1969) and have been confirmed in Jones

(1984). There are slight differences in the modern forms (particularly the nature of the multicellular “glandular” trichomes) that usually allow modern forms to be distinguished, but there are no consistent generically correlated features that can be used to assign a fossil form to an extant genus with confidence. As with all forms, cuticular information greatly enhances the chances of correctly classifying a fossil leaf type. Kräusel and Weyland (1950), for instance, used cuticular evidence to justify transfer of a fossil putative chestnut oak *Q. furcinervis* (Rossm.) Unger to the genus *Castanopsis*. Although I do not share the certainty with which Kräusel and Weyland made the transfer, the cuticle information does support their position. If the nature of the trichomes, not just the trichome bases, were known, such a transfer might be made with assurance.

Although the true affinities of many putatively fagaceous fossil leaves remain to be established, different leaf forms appear to have arisen at different times in this family. The entire and holly-like leaves from the Upper Cretaceous and Paleocene may be from the first *Quercus* species. Coarsely round-toothed and regular chestnut oak types do not appear until the Eocene. Lobed forms first occur in the Oligocene and become common in the Miocene. A thorough reexamination of fossil fagaceous leaves is needed, however, to confirm the affinities of these fossils and help resolve questions about the origin and subsequent evolution of *Quercus*.

FINAL DISCUSSION AND CONCLUSIONS

Leaves of the Fagaceae vary considerably within broad limits. All extant Fagaceae have simple leaves of high rank with obliquely oriented tertiary veins, anomocytic and/or cyclocytic stomatal complexes, and specific trichome complements, which depend on the intrafamilial taxon in question. Nearly all fagaceous leaves can be classified into one of the following major morphotypes: 1) entire or partially toothed, elliptical to lanceolate evergreen forms; 2) entire, broad, tardily deciduous to evergreen forms; 3) xeromorphic, sclerophyllous, small, entire-margined, evergreen forms; 4) sclerophyllous holly-like forms; 5) craspedodromous “chestnut”-like forms; 6) coarsely round-toothed, deciduous forms; 7) roundly lobed deciduous forms; 8) sharply lobed deciduous forms; and 9) narrow willow-like leaves. Many of these leaf types, however, cross taxonomic boundaries, and there is

considerable foliar variability among intrafamilial taxa.

Leaves of extant Fagaceae can be distinguished from those of other families when cuticular and architectural features are available, but the intrafamilial taxonomic utility is somewhat limited because of the variability of foliar characters. Leaves of most Fagaceae can be classified at the species or species complex level. Unfortunately, leaf character differences often do not coincide with established subfamilial, generic, subgeneric, and even sectional boundaries. Thus, it is sometimes impossible to separate these intermediate level taxa without including more than one character assemblage of subordinate taxa. Some features or groups of characters are unique to specific taxa whereas other foliar syndromes can be found among several. Entire-margined evergreen leaves with type 9 trichomes, for instance, are found only in the genus *Lithocarpus* whereas regularly toothed, craspedodromous, chestnut-like leaves with types 5, 6 and 15 and/or 16 trichomes, are found in four genera and two subfamilies. Thus, classification among various intrafamilial taxa can be easy to impossible, depending on the uniqueness of the character assemblage of the leaf at hand.

Foliar information, when combined with other taxonomically useful data, contributes to our understanding of the taxonomy of this family. A classification scheme based on foliar and other data is presented in Table 2. This proposed classification scheme differs in some respects from the widely accepted scheme proposed by Forman (1966a). Leaf data, for instance, indicate that *Nothofagus* is distinct from all other Fagaceae and is, instead, closer to the Betulaceae. The doubly serrate margins and large glandular trichomes, common to *Nothofagus* and members of the Betulaceae, are rare or absent in all other modern Fagales. A distinction between *Nothofagus* and the Fagaceae sensu stricto is also apparent when pollen (Praglowksi, 1982), chromosome numbers (Armstrong & Wylie, 1965), inflorescences (Reece, 1938), vegetative features such as wood (Shimaji, 1962), and phytochemical data (Oesch, 1969) are examined. Foliar information, together with that mentioned above, supports recognition of the Nothofagaceae as proposed by Kuprianova (1962) and Nixon (1982) and suggests the phylogenetic relationships illustrated in Text-Figure 5. Foliar information tells us little, however, about the intrageneric taxonomy of this genus. The entire-

TABLE 2. Proposed classification of genera traditionally considered to be fagaceous.

Nothofagaceae	Fagaceae			
	Fagoideae	Castaneoideae	Trigonobalanoideae	Quercoideae
<i>Nothofagus</i>	<i>Fagus</i>	<i>Castanea</i> <i>Chrysolepis</i> <i>Castanopsis</i> <i>Lithocarpus</i>	<i>Trigonobalanus</i> ^a	<i>Quercus</i>

^a *Trigonobalanus* is a heterogeneous assemblage that should be divided when a more complete knowledge of the component species is obtained.

margined tropical forms (i.e., those of the ‘brassi’ pollen group) do seem to be a tightly knit unit, but little correlation can be found between the various lines of morphological and anatomical evidence in other groups. The lack of correlation between various lines of morphological and anatomical evidence has been noted by previous authors (Hanks & Fairbrothers, 1976). Thus, if one accepts the Nothofagaceae, recognition of the ‘brassi’ group as a separate genus could be justified but it would be hard to support further division of the remaining species at this level.

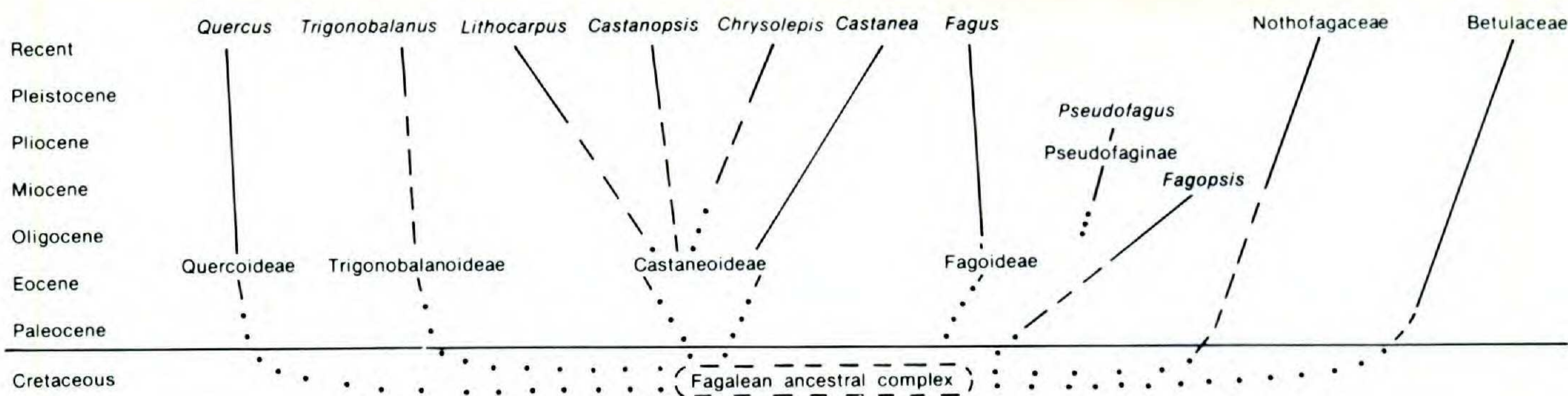
Fagus, often thought to be closely related to *Nothofagus*, is clearly distinguishable from this and other genera of Fagaceae and thus should be retained in its own subfamily, the Fagoideae. The uniformity of the leaves in this genus supports the lack of formal division into subgenera or sections. The leaves of the Quercoideae and Castaneoideae are most often distinguishable. However, certain forms like the “chestnut” leaf type are found in both subfamilies. This foliar overlap may be used in support of the recognition of a single subfamily, the Castaneoideae, as suggested most recently by Brett (1964). Overlap in wood anatomy, fruit, and cupule structure also obscures the distinction between these two subfamilies. Pollen morphology provides convincing evidence, however, for separating these two taxa. Another problem, at the subfamilial level, is the proposed recognition of the Trigonobalanoideae (Lozano-C. et al., 1979). The foliar characteristics of *Trigonobalanus* (e.g., tooth type, trichome complements) are sufficiently distinct from those of other Quercoideae to rationalize inclusion in a separate subfamily when considered in light of differences in chromosome numbers as well as the morphological and anatomical features reviewed by Lozano-C. et al. (1979). Removal of *Trigonobalanus* from the Quercoideae would also help sharpen the distinction between the Quercoideae and the Castaneoideae. Within *Trigo-*

nobalanus there is sufficient foliar diversity to support further separation of this genus into discrete subgenera or even separate genera, as proposed by Erdtman (1967) on the basis of pollen form and structure.

Quercus presents numerous taxonomic problems. The division of *Quercus* into several genera, as proposed by Schwarz (1936a), is not warranted by foliar data. The intrasectional variability is great in nearly all sections and there is a great deal of overlap. The subgenus *Cyclobalanopsis* as proposed by Camus (1934–1954) is a rather discrete unit and probably merits its subgeneric status. The sections of the subgenus *Quercus* show general trends in foliar features, but the sections cannot be discretely separated using leaf characters alone.

Foliar features generally confirm the current consensus concerning generic delimitation within the Castaneoideae. *Chrysolepis* is clearly differentiable from *Castanopsis* on the basis of differences in leaf architecture and trichome complements. This supports the conclusions of Hjelmqvist (1948), Forman (1966b), and many other modern authors, who base their conclusions primarily on reproductive features. *Castanea* is a uniform and well defined taxon. The leaves share the uniformity characteristic of nearly all organs of this genus. There is little difference in the leaves, even between the two sections, *Eucastanon* and *Balanocastanon*, of this genus. Unfortunately, a few members of *Lithocarpus*, *Castanopsis*, and even *Quercus* possess the same general leaf architectural and cuticular features making identification to the generic level difficult.

In *Castanopsis* there are few differences among the leaves of most sections, and thus foliar features cannot be used to support these sectional divisions. Foliar data do support retention of the *Castanopsis fissa* group within *Castanopsis* rather than placement in *Lithocarpus*. This is in ac-



TEXT-FIGURE 5. Possible phylogenetic relationships within the Fagales.

cordance with the findings of Luong (1965) and Forman (1966b) based on infructescence studies.

It is apparent that *Lithocarpus* is a large and relatively unstudied genus that requires further taxonomic revision. The leaves of this group, as currently circumscribed, are fairly uniform in gross morphology but trichome differences, particularly the absence of type 9 trichomes in relatively few specimens, provide incentive for the much needed revision of this group. It does appear that *Lithocarpus densiflorus* stands apart from all other members of this genus and there is some indication that *Limlia* may deserve recognition as a separate genus. Additional conclusions concerning the impact of foliar data on the classification of other infrageneric taxa in this and some other genera of Fagaceae must await analysis of a more complete sample.

The potential for identifying and correctly classifying fossil fagaceous leaves diminishes as the age of the material increases. Although this is substantially intuitive, the age at which one must use extreme caution when assigning materials to modern genera or subfamilies is much more recent than one might have expected only a decade ago. The recent discovery of *Pseudofagus* (Smiley & Huggins, 1981) and the reinterpretation of *Fagopsis* (Manchester & Crane, 1983) serve to illustrate that leaves similar to those of extant genera can be found on plants of extinct genera and subfamilies, in sediments as young as the Miocene. The strength of any determination based on leaves must therefore rest substantially on correlation with fossils of other more definitive organs. The ability to determine the affinities of more recent materials will depend, as with modern leaves of this family, on how unique the particular leaf type is within the family.

The time and place of origin of the Fagaceae is still largely a mystery. No leaves or other organs definitely assignable to the Fagaceae have

been found prior to the Eocene. The diversity present in the Eocene, however, suggests an origin at least as early as the Paleocene. The existence of primitive Fagaceae, or possible precursors thereof, in the Cretaceous (Santonian) of North America is indicated by the recent discovery of a "fagalean" flower by Friis (pers. comm.) and Tiffney (pers. comm.). The ability to identify early remains as Fagaceae may well be limited by the existence of vegetative and reproductive strategies, such as wind and/or water fruit dispersal, alien to modern Fagaceae with which we are familiar. The modern large animal dispersed fruits, that is, acorns, chestnuts, and beechnuts, do not appear until the Eocene (Tiffney, 1984). Their development was probably a function of coevolution with small mammals, for example, rodents. Rodents first appear in the uppermost Paleocene and squirrels, which commonly disperse modern fagaceous fruits, evolved in the late Eocene (Romer, 1966). It is reasonable to assume then that Paleocene and earlier forms would have gross fruit morphologies unlike those of modern members of the family. Similar trends in fruit evolution occur in the Juglandaceae (Manchester, 1981b) and most likely the Betulaceae as well.

Most modern authors contend that the Fagaceae arose in the Northern Hemisphere late in the Cretaceous. The presence of *Nothofagus* in the Southern Hemisphere does not contradict this conclusion if one considers the relation of this taxon to the Fagaceae sensu stricto and the Betulaceae. If *Nothofagus* is closer to the Betulaceae and merits distinction as a separate family, it more than likely evolved independently from a common fagalean ancestor during the late Cretaceous. This ancestor or ancestral complex probably extended its range southward, or northward according to Schuster (1972), at or prior to this time. This migration may well have occurred through Africa, as Raven and Axelrod (1974)

have suggested. Examination of the Upper Cretaceous floras of Africa for evidence of fagalean fossils is needed to help test this hypothesis.

The known fossil record suggests that the Nothofagaceae evolved from this primitive fagalean complex in the Southern Hemisphere (probably in southern Australia or Antarctica) while the Fagaceae sensu stricto evolved from representatives of the same complex in the Northern Hemisphere. The fossil record indicates, with minor recent exceptions, that neither family has occurred in any hemisphere other than that in which it is found today. It is extremely difficult to be more specific about the place in which the Fagaceae sensu stricto evolved. It has been noted that American forms of both *Fagus* and *Quercus* have been found previously in Europe and that European forms have not been found in North America. It also seems that the greatest diversity has existed on the Eurasian land mass. Whether diversity is a good indicator of the site of origin of a taxon remains to be proven. The fossil record, upon which final resolution of this problem must depend, is not known well enough to confirm southeast Asia, as many have suggested, or any other hypothesized locus, as the site of origin for the Fagaceae.

We know little more about the nature of the first Fagaceae. When the first firm record of the Fagaceae appears (in the Eocene) we have both the Castaneoideae and Quercoideae represented in fairly modern form. The first records of modern genera are *Castanea* and *Quercus*, but neobotanists have generally considered these to be derived forms within the family. *Lithocarpus*, *Castanopsis*, *Chrysolepis*, and *Trigonobalanus* are the genera that are usually cited as candidates for evolutionary 'Urpflanzen' within this group. Given the different selective pressures, particularly those associated with fruit dispersal, it seems likely that the earliest Fagaceae would be different from all modern genera. *Fagopsis* fits the idealistic image of a primitive fagaceous form but reproductive material has been confirmed only in the Eocene and early Oligocene, too late to indicate ancestral affinities. If, however, Paleocene leaves assigned to *Q. groenlandica* can be shown to be *Fagopsis*, as Wolfe (1977) suggested, this genus would likely be part of the ancestral fagaceous complex.

When the mutual characteristics of the Betulaceae, *Nothofagus*, and the Fagaceae sensu stricto are considered, we might expect the ancestral plexus to consist of wind dispersed "amentifer-

ous" forms with irregularly toothed (perhaps doubly serrate), craspedodromous, simple leaves. Such leaves have been found in the late Cretaceous and have been attributed to the Betulaceae (Wolfe, 1973). Crane (1981), however, indicated that the first solid evidence of the existence of the Betulaceae occurs in the Paleocene. Whether or not these leaves are betulaceous, fagaceous, *Nothofagus*, or some fagalean intermediate can be determined only when reproductive materials are found and analyzed.

There does seem to be a pattern to the appearance of various leaf forms in the Fagaceae. If we disregard the Cretaceous leaf forms as suggested by Wolfe (1973), the first fagaceous leaves appear to be irregularly serrate, simple, pinnate forms with percurrent tertiaries obliquely disposed in relation to the midrib. Many of these occur in the Paleocene and have been placed in the genus *Dryophyllum* by previous workers. During the Eocene we have the appearance of the "chestnut" leaf type and coarsely round-toothed oak leaves. The first sharply lobed oaks appear in the Oligocene and become abundant in the Miocene. The earliest record of round-lobed leaves occurs in the Miocene where they are particularly abundant in Eurasia. Because of numerous homeomorphies, it is difficult to know which of the fossil holly-like forms and laurel forms are truly fagaceous. In spite of their alleged antiquity, fagaceous holly-like forms may not have arisen until the climatic deterioration at the end of the Eocene and did not become abundant until the Miocene. It is also impossible to know which of the laurel-like and other entire-margined forms are fagaceous until the nature of their cuticles has been determined.

Rüffle and co-workers (see Rüffle, 1980) have proposed the only phylogenetic model for this group based on leaves. They maintained, largely on the basis of cuticular resemblance, that the Fagaceae or fagalean ancestors extend back into the Cretaceous where they blend with the palmately lobed and palmately compound *Debeya-Dewalquea* complex. According to this hypothesis, these types form a bridge between the palmate platanoid complex and the pinnate fagaceous types with which we are familiar. Rüffle and Knappe (1977) also contended that the lobed oaks, for example, *Q. falcata*, are atavistic expressions of the early platanoid types. This is a very intriguing hypothesis, which may be correct, yet the cuticular evidence that these workers cite is not very strong. No trichome data are

offered and the characters that are consistent with those of the Fagaceae (e.g., anomocytic stomatal complexes) are common to many other taxa as well. The validity of this proposal must be tested by rigorous examination of relevant fossil leaf forms in conjunction with the pioneering work on reproductive materials being conducted by Crepet, Daghljan, Manchester, and others.

LITERATURE CITED

- ABBE, E. C. 1974. Flowers and inflorescences of the "Amentiferae." Bot. Rev. (Lancaster) 40: 159–261.
- AGUIRRE, A. C. & E. J. ROMERO. 1982. Arquitectura foliar de las especies australianas y neocelandesas de *Nothofagus* (Fagaceae). Bol. Soc. Argent. Bot. 20: 227–240.
- AMES, H. & W. RIEGEL. 1962. Palynological investigation of coals from the Chickatoo Formation, Alaska. Pollen & Spores 4: 328 [Abstract.]
- ANDREÁNSKY, G. 1966. On the Upper Oligocene flora of Hungary. Stud. Biol. Hung. 5: 1–151.
- & KOVACS-SONKODY (editors). 1955. Gleiderung und Ökologie der jüngeren Tertiärfloren Ungarns. Magyar Állami Földt. Intéz. Évk. 44: 1–326.
- ARCHANGELSKY, S. & E. ROMERO. 1974. Los registros mas antiguos del polen de *Nothofagus* (Fagaceae) de Patagonia (Argentina & Chile). Bol. Soc. Bot. México 33: 13–30.
- ARMSTRONG, J. M. & A. P. WYLIE. 1965. A new basic chromosome number in the family Fagaceae. Nature 205: 1340–1341.
- AXELROD, D. I. 1944. The Sonoma flora (California). In R. W. Chaney (editor), Pliocene Floras of California and Oregon. Publ. Carnegie Inst. Wash. 553: 167–206.
- . 1956. Mio-Pliocene floras from west central Nevada. Univ. Calif. Publ. Geol. Sci. 33: 1–322.
- . 1964. The Miocene Trapper Creek flora of southern Idaho. Univ. Calif. Publ. Geol. Sci. 51: 1–181.
- . 1966. The Eocene Copper Basin flora of northeastern Nevada. Univ. Calif. Publ. Geol. Sci. 59: 1–125.
- & P. H. RAVEN. 1978. Late Cretaceous and Tertiary vegetation history of Africa. Pp. 79–130 in M. J. Werner (editor), Biogeography and Ecology of Southern Africa. Junk Publ., The Hague.
- BAAS, P. 1982. Comparative leaf anatomy of *Trigonobalanus* Forman Fagaceae. Blumea 28: 171–175.
- BANDULSKA, H. 1923. A preliminary paper on the cuticular structure of certain dicotyledonous and coniferous leaves from the Middle Eocene flora of Bournemouth. J. Linn. Soc., Bot. 46: 241–269.
- . 1924. On the cuticles of some recent and fossil Fagaceae. J. Linn. Soc., Bot. 46: 427–441.
- BARNETT, E. C. 1944. Keys to the species groups of *Quercus*, *Lithocarpus* and *Castanopsis* of eastern Asia, with notes on their distribution. Trans. Bot. Soc. Edinburgh 34: 159–204.
- BENSON, L. 1962. Plant Taxonomy: Methods and Principles. Ronald Press Co., New York.
- BENTHAM, G. & J. D. HOOKER. 1880. Genera Plantarum, Volume 3, Part 1. L. Reeve & Co., London.
- BERRY, E. W. 1916. Lower Eocene floras of southeastern North America. Profess. Pap. U.S. Geol. Surv. 91: 1–481.
- . 1923. Tree Ancestors. Williams & Wilkins Co., Baltimore.
- . 1938. Tertiary flora from the Rio Pichileufu, Argentina. Special Pap. Geol. Soc. Amer. 12: 1–149.
- . 1945. The Lower Eocene flora of southeastern North America. J. Wash. Acad. Sci. 35: 87–89.
- BEYER, A. F. 1954. Some petrified wood from the Specimen Ridge Area of Yellowstone National Park. Amer. Midl. Naturalist 51: 553–567.
- BEYN, W. 1940. Die Einschaltung geformter Pflanzenreste in das Braunkohlenprofil des mittleren Geiseltales. Nova Acta Leop. n.s. 8: 377–438.
- BOESHORE, I. & J. A. JUMP. 1938. A new fossil oak from Idaho. Amer. J. Bot. 25: 307–311.
- BONES, T. J. 1979. Atlas of fossil fruits and seeds from north central Oregon. Oregon Mus. Sci. Industr. Occas. Pap. Nat. Sci. 1: 1–23.
- BOUREAU, E. & M. SALARD. 1960. Contribution a l'étude paleoxylologique de la Patagonie (I). Senckenberg. Leth. 41: 297–315.
- BRAY, J. R. 1960. A note on hybridization between *Quercus macrocarpa* Michx. and *Quercus bicolor* Willd. in Wisconsin. Canad. J. Bot. 38: 701–704.
- BRENNER, W. 1902. Klima und Blatt bei der Gattung *Quercus*. Flora 90: 114–160.
- BRETT, D. W. 1960. Fossil oak wood from the British Eocene. Palaeontology 3: 86–92.
- . 1964. The inflorescence of *Fagus* and *Castanea*, and the evolution of the cupules of the Fagaceae. New Phytol. 63: 96–118.
- BROWN, R. W. 1944. Temperate species in the Eocene flora of the southeastern United States. J. Wash. Acad. Sci. 34: 349–351.
- BURGER, W. C. 1975. The species concept in *Quercus*. Taxon 24: 45–50.
- CAMUS, A. 1928–1929. Encyclopédie Économique de Sylviculture, Volume 3, Les Châtaigniers. Monographie des *Castanea* et *Castanopsis*. Académie des Sciences, Paris.
- . 1934–1954. Encyclopédie Économique de Sylviculture, Volumes 6–8, Les Chênes. Monographie du Genre *Quercus* (et *Lithocarpus*). Académie des Sciences, Paris.
- . 1951. Le genre *Nothofagus*. Rev. Int. Bot. Appl. Agric. Trop. 31: 71–84.
- CANDOLLE, A. DE. 1868. Prodrôme Systematis Naturalis Regni Vegetabilis. Cupuliferae, Part 16(2). Victoris Masson & Filii, Paris.
- CHANDLER, M. E. 1957. The Oligocene flora of the Bovay Tracy Lake Basin, Devonshire. Bull. Brit. Mus. (Nat. Hist.), Geol. 3: 73–123.
- . 1964. The Lower Tertiary Floras of Southern England IV. British Museum (Natural History), London.
- CHANEY, R. W. 1944. The Dalles flora. In R. W. Chaney (editor), Pliocene Floras California and Oregon. Publ. Carnegie Inst. Wash. 553: 285–322.
- (editor). 1963. Tertiary Flora of Japan. Collaborating Association to Commemorate the 80th

- Anniversary of the Geological Survey of Japan, Tokyo.
- & E. I. SANBORN. 1933. The Goshen flora of west central Oregon. Publ. Carnegie Inst. Wash. 439: 1–103.
- CHINESE NEOGENE PLANT EDITORIAL GROUP. 1978. Chinese Fossil Plants, Volume 3, Chinese Neogene Plants. Academia Sinica, Beijing Plant Research Institute. Science Press, Beijing.
- CHMURA, C. A. 1973. Upper Cretaceous (Campanian-Maestrichtian) angiosperm pollen from the Western San Joaquin Valley, California. U.S.A. Palaeontographica, Abt. B, Paläophytol. 141: 89–171.
- CONWENTZ, H. 1886. Die Flora des Bernsteins. Zweiter Band: Die Angiospermen des Bernsteins. Engelmann, Danzig.
- COOKSON, I. 1958. Fossil pollen grains of *Nothofagus* from Australia. Proc. Roy. Soc. Victoria 71: 25–30.
- & K. M. PIKE. 1955. The pollen morphology of *Nothofagus* Bl. subsection *Bipartitae* Steen. Austral. J. Bot. 3: 197–206.
- COOPER, A. W. & E. P. MERCER. 1977. Morphological variation in *Fagus grandifolia* Ehrh. in North Carolina. J. Elisha Mitchell Sci. Soc. 93: 136–149.
- CORNER, E. J. 1939. Notes on the systematy and distribution of Malayan phanerogams. Gard. Bull. Straits Settle. 10: 239–329.
- COUPER, R. A. 1953. Distribution of Proteaceae, Fagaceae and Podocarpaceae in some Southern Hemisphere Cretaceous and Tertiary Beds. New Zealand J. Sci. Technol. 35: 247–250.
- . 1960a. Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their paleogeographic significance. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 152: 491–500.
- . 1960b. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand Geol. Surv. Bull. 32: 1–87.
- COZZO, D. 1950. Estudio del leño fosil de una Dicotiledonea de la Argentina *Nothofagoxylon neuquenense*. Comun. Inst. Nac. Invest. Ci. Nat., Ser. Ci. Bot. 1: 3–12.
- CRANE, P. R. 1978. Angiosperm leaves from the Lower Tertiary of southern England. Cour. Forsch.-Inst. Senckenberg 30: 126–132.
- . 1981. Betulaceous leaves and fruits from the British Upper Paleocene. Bot. J. Linn. Soc. 83: 103–136.
- CRANWELL, L. M. 1939. Southern beech pollens. Rec. Auckland Inst. Mus. 2: 175–196.
- . 1959. Fossil pollen from Seymore Island, Antarctica. Nature 184: 1782–1785.
- . 1963. *Nothofagus*: living and fossil. In J. K. Gressitt (editor), Pacific Basin Biogeography Symposium. Bishop Museum Press, Honolulu.
- . 1964. Antarctica: cradle or grave for its *Nothofagus*. Pp. 87–93 in L. M. Cranwell (editor), Ancient Pacific Floras. Univ. of Hawaii Press, Honolulu.
- CREPET, W. L. & C. P. DAGHLIAN. 1980. Castaneoid inflorescences from the Middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. Amer. J. Bot. 67: 739–757.
- & M. S. ZAVADA. 1983. Quercoid catkins from the Middle Eocene. Amer. J. Bot. 70(5, 2): 70. [Abstract.]
- CROIZAT, L. 1952. Manual of Phytogeography. W. Junk, The Hague.
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- CROVELLO, T. J. 1976. Numerical approaches to the species problem. Pl. Syst. Evol. 125: 179–187.
- CUTLER, D. F. 1964. Anatomy of vegetative organs of *Trigonobalanus* Forman (Fagaceae). Kew Bull. 17: 401–409.
- DADSWELL, H. E. & H. D. INGLE. 1954. The wood anatomy of the New Guinea *Nothofagus* Bl. Austral. J. Bot. 2: 141–153.
- DAGHLIAN, C. P. & W. L. CREPET. 1983. Oak catkins, leaves and fruits from the Oligocene Catahoula Formation and their evolutionary significance. Amer. J. Bot. 70: 639–649.
- DARLINGTON, P. J. 1965. Biogeography of the Southern End of the World. Harvard Univ. Press, Cambridge.
- DETTMANN, M. E. & G. PLAYFORD. 1969. Taxonomy of some Cretaceous spores and pollen grains from eastern Australia. Proc. Roy. Soc. Victoria, n.s. 81: 69–93.
- DILCHER, D. L. 1973. A revision of the Eocene flora of southeastern North America. Palaeobotanist 20: 7–18.
- . 1974. Approaches to the identification of angiosperm leaf remains. Bot. Rev. (Lancaster) 40: 1–157.
- DODE, L. A. 1908. Notes dendrologiques sur les châtaigniers. Bull. Soc. Dendrol. France 8: 140–159.
- DORF, E. 1938. A late Tertiary flora from southwestern Idaho. In Miocene and Pliocene Floras of Western North America. Publ. Carnegie Inst. Wash. 476: 73–124.
- . 1960. Tertiary forests of Yellowstone National Park Wyoming. Pp. 253–260 in Billings Geological Society Guidebook, 11th Annual Field Conference, Billings Geological Society, Billings.
- . 1964. The petrified forests of Yellowstone Park. Amer. Sci. 210: 105–114.
- DUSÉN, P. 1899–1902. Über die tertiäre Flora der Magellansländer. Svenska Exped. Megellansländerna 1895–1897, 1: 87–107, 241–248.
- . 1908. Über die tertiäre Flora der Seymour-Insel. Wiss. Ergebn. Schwed. Südpolarexped. 1901–1903, 3: 1–27.
- DYAL, S. C. 1936. A key to the species of oaks of eastern North America based on foliage and twig characters. Rhodora 38: 53–63.
- EAMES, A. J. 1910. On the origin of the broad ray in *Quercus*. Bot. Gaz. (Crawfordsville) 49: 161–166.
- EDWARDS, W. N. 1931. Dicotyledons (Ligna). Part 17. In W. Jongmans (editor), Fossilium Catalogus II: Plantae. W. Junk, Berlin.
- ELIAS, T. S. 1971. The genera of Fagaceae in the southeastern United States. J. Arnold Arbor. 52: 159–195.
- ELSIK, W. C. 1974. *Nothofagus* in North America. Pollen & Spores 16: 285–299.
- ERDTMAN, G. 1943. An Introduction to Pollen Analysis. Ronald Press, New York.
- . 1967. On the pollen morphology of *Trigonobalanus* (Fagaceae). Bot. Not. 120: 324–333.

- ETTINGSHAUSEN, C. F. VON. 1887a. Beiträge zur Kenntniss der Tertiärflora Australiens. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 54: 81–142.
- . 1887b. Beiträge zur Kenntniss der Tertiärflora Neuseelands. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 54: 143–192.
- . 1888. Contributions to the Tertiary flora of Australia. Mem. Geol. Surv. New South Wales, Palaeontol. 2: 1–189.
- . 1891. Über tertiäre *Fagus*-arten der südlichen Hemisphäre. Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt., 1, 100: 114–137.
- . 1896. Über die Nervation der Blätter bei der Gattung *Quercus*, mit besonderer Berücksichtigung ihrer vorweltlichen Arten. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 63: 117–180.
- FERGUSON, D. K. 1971. The Miocene flora of Krezau, western Germany. 1. The leaf-remains. Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 60: 1–297.
- FEY, B. S. & P. K. ENDRESS. 1983. Development and morphological interpretation of the cupule in Fagaceae. *Flora* 173: 451–468.
- FORMAN, L. L. 1962. A new genus in the Fagaceae. *Taxon* 11: 139–140.
- . 1964a. *Trigonobalanus* a new genus of Fagaceae, with notes on the classification of the family. *Kew Bull.* 17: 381–396.
- . 1964b. *Trigonobalanus* and its importance in the taxonomy of the Fagaceae. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 161: 48–49.
- . 1966a. On the evolution of cupules in the Fagaceae. *Kew Bull.* 18: 385–419.
- . 1966b. Generic delimitation in the Castaneoideae. *Kew Bull.* 18: 421–426.
- & D. F. CUTLER. 1967. Additional notes on *Trigonobalanus* (Fagaceae). *Kew Bull.* 21: 331–337.
- FRENGUELLI, J. 1941. Nuevos elementos florísticos del Megellaniano de Patagonia austral. *Notas Prelim. Mus. La Plata* 6: 173–202.
- GAZEAU, F. & J. C. KOENIGUER. 1968. Les bois hétéroxyles du Mio-Pliocene de Touraine. *Com. Trav. Hist. Sci., Mem. Sect. Sci. Paleobot.* 2: 56–69.
- GOEPPERT, H. R. 1855. Die Tertiäre Flora von Schosnitz in Schlesien. *Görlitz*.
- GOTHAN, W. 1908. Die fossilen Hölzer von der Seymour und Snow Hill-Insel. *Wiss. Ergebn. Schwed. Südpolarexped. 1901–1903*, 3: 1–33.
- GREGOR, H. J. 1980. Die Miozänen Frucht- und Samen-Floren der Ober-pfalzer Braunkohle II. Funde aus den Kohlen und tonigen Zwischenmitteln. *Palaeontographica*, Abt. B, Paläophytol. 174: 7–94.
- GROS, J. 1983. Nouveau bois fossile de l'Eggenburgien d'Autriche: *Quercoxylon furwaldense* n.sp. *Rev. Gén. Bot.* 90: 43–80.
- GRUAS-CAVAGNETTO, C. 1978. Étude palynologique de l'Eocene du Bassin Anglo-Parisien. *Mem. Soc. Geol. France*, n.s. 56: 1–64.
- GUO, S.-X. 1980. Late Cretaceous and Eocene floral provinces. In *First Conf. of the International Organization for Paleobotany*, Reading, England. Academia Sinica (Inst. Geol. Palaeontol.), Nanjing.
- HANKS, S. L. & D. E. FAIRBROTHERS. 1976. Palynotaxonomic investigation of *Fagus* L. and *Nothofagus* Bl.: light microscopy, scanning electron microscopy and computer analyses. *Bot. Syst.* 1: 1–142.
- HARDIN, J. W. 1975. Hybridization and introgression in *Quercus alba*. *J. Arnold Arbor.* 56: 336–363.
- . 1976. Terminology and classification of *Quercus* trichomes. *J. Elisha Mitchell Sci. Soc.* 92: 151–161.
- . 1979. Patterns of variation in foliar trichomes of eastern North American *Quercus*. *Amer. J. Bot.* 66: 576–585.
- HEER, O. 1869. Miocene baltische Flora. *Beitr. Naturk. Preussens* 2: 1–104.
- . 1870. Die Miocene flora and fauna Spitzbergens. *Kongl. Svenska Vetensk. Acad. Handl.* 8: 1–98.
- . 1883. *Flora fossilis arctica*. Die fossile flora Grönlands, Part 2. J. Wurster and Co., Zurich.
- HERNÁNDEZ-COMACHO, J., G. LOZANO-C. & J. E. HENAO-S. 1980. Hallazgo del género *Trigonobalanus* Forman, 1962 (Fagaceae) en el neotropico-II. *Caldasia* 13: 9–43.
- HICKEY, L. J. 1973. Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.* 60: 17–33.
- . 1977. Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of western North Dakota. *Mem. Geol. Soc. Amer.* 150: 1–181.
- . 1979. A revised classification of the architecture of dicotyledonous leaves. In C. R. Metcalfe & L. Chalk (editors), *Anatomy of the Dicotyledons*, 2nd edition. Clarendon Press, Oxford.
- & J. A. WOLFE. 1975 [1976]. The bases of angiosperm phylogeny: Vegetative morphology. *Ann. Missouri Bot. Gard.* 62: 538–589.
- , R. M. WEST & M. R. DAWSON. 1984. Arctic biostratigraphic heterochroneity. *Science* 224: 175–176. [Letter.]
- , ———, ——— & D. K. CHOI. 1983. Arctic terrestrial biota: paleomagnetic evidence of age disparity with mid-northern latitudes during the late Cretaceous and early Tertiary. *Science* 221: 1153–1156.
- HILL, R. S. 1983a. *Nothofagus* macrofossils from the Tertiary of Tasmania. *Alcheringa* 7: 169–183.
- . 1983b. Evolution of *Nothofagus cunninghamii* and its relationship to *Nothofagus moorei*: as inferred from Tasmanian macrofossils. *Austral. J. Bot.* 31: 453–465.
- HJELMQVIST, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Not. Suppl.* 2: 1–171.
- HOLLICK, A. 1936. The Tertiary floras of Alaska. *Profess. Pap. U.S. Geol. Surv.* 182: 1–185.
- HOLLOWAY, J. 1954. Forests and climates in the South Island of New Zealand. *Trans. & Proc. Roy. Soc. New Zealand* 82: 329–410.
- HOPKINS, W. S. 1969. Palynology of the Eocene Kitsilano Formation, southwest British Columbia. *Canad. J. Bot.* 47: 1101–1131.
- HOU, D. 1971. Chromosome numbers of *Trigonobalanus verticillata* Forman (Fagaceae). *Acta Bot. Neerl.* 20: 543–549.
- HSU, Y.-C. & H.-W. JEN. 1979. New species and new combinations of Fagaceae from China. *Acta Bot.*

- Yunn. 1: 146–148. [In Chinese. Examined in abstract form, Biol. Abstr. 71: 6015.]
- HU, H. H. & R. W. CHANEY. 1940. A Miocene flora from Shantung Province, China, Part I, Introduction and systematic considerations. *Palaeontol. Sin.*, n.s. A, 1: 1–83.
- HUMMEL, A. 1983. The Pliocene leaf flora from Ruzow near Zary in Lower Silesia, SW Poland. *Prace Muz. Ziemi* 36: 9–104.
- HUMPHRIES, C. J. 1981. Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). Pp. 177–207 in V. A. Funk & D. R. Brooks (editors), *Advances in Cladistics*. New York Botanical Garden, New York.
- HUTCHINSON, J. 1967. *The Genera of Flowering Plants*, Volume 2. Clarendon Press, Oxford.
- JARZEN, D. M. & G. NORRIS. 1975. Evolutionary significance and botanical relationships of Cretaceous angiosperm pollen in the western Canadian interior. *Geosci. & Man* 11: 47–60.
- JENSEN, R. J. & W. H. ESHBAUGH. 1976. Numerical taxonomic studies of hybridization in *Quercus*. *Syst. Bot.* 1: 1–19.
- JONES, J. H. 1984. Leaf Architectural and Cuticular Analyses of Extant Fagaceae and 'Fagaceous' Leaves From the Paleogene of Southeastern North America. Ph.D. thesis. Indiana Univ., Bloomington.
- JUNG, W., E. KNOBLOCH, Z. KVAČEK & A. SELMEIER. 1971. Makrofloristische Untersuchungen in Braunkohlentertiär der Oberpfalz. *Mitt. Bayer. Staatssamml. Palaontol. Hist. Geol.* 11: 223–249.
- JUSSIEU, A. L. DE. 1789. *Genera Plantarum*. Wheldon & Wesley, New York. [1964 Reprint.]
- KAUL, R. B. & E. C. ABBE. 1984. Inflorescence architecture and evolution in the Fagaceae. *J. Arnold Arbor.* 65: 375–401.
- KEDVES, M. 1964. Sporomorphs nouveaux des couches Eocenes de Hongrie. *Pollen & Spores* 6: 195–201.
- . 1967. Sur quelques problèmes de stratigraphie palynologique appliqué au Tertiaire inférieur en Europe. *Pollen & Spores* 9: 321–334.
- . 1978. Palynological investigations into sediments of the lower Paleogene period in Bulgaria. *Acta Biol. (Szeged 1955+)* 24: 23–30.
- KENT, D. V., M. C. MCKENNA, N. D. OPDYKE, J. J. FLYNN & B. J. MACFADDEN. 1984. Arctic biostratigraphic heterochroneity. *Science* 224: 173–174. [Letter.]
- KIRCHHEIMER, F. 1957. *Der Laubgewachse der Braunkohlenzeit*. Veb Wilhelm Knapp, Halle.
- KNOBLOCH, E. 1969. Tertiäre Floren von Mähren. Moravské Museum, Brno.
- KOCH, B. E. 1963. Fossil plants from the Lower Paleocene of the Agatdalen (Angmartussut) area, central Nugsuaq Peninsula, Northwest Greenland. *Meddel. Grønland* 172: 1–120.
- KOVACS, E. E. 1961. Untersuchungen und ungarischen Eichen des Tertiärs. I. Samartische Eichen. *Acta Bot. (Szeged 1955+)* 8: 283–302.
- KRASSER, F. 1903. Konstantin von Ettingshausen's Studien über die fossile Flora von Ouricango in Brasilien. *Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1*, 112: 852–860.
- KRÄUSEL, R. 1924. Beiträge zur Kenntnis der fossilen Flora Südamerikas. I. Fossile Hölzer aus Patagonien und benachbarten Gebieten. *Ark. Bot.* 19: 1–36.
- . 1939. Ergebnisse der Forschungsreisen Prof. E. Stromer's in den Wüsten Ägyptens, IV. Die fossilen Floren Ägyptens. *Abh. Bayer. Akad. Wiss., Math.-Naturwiss. Abt.* 47: 1–140.
- & H. WEYLAND. 1950. Kritische Untersuchungen zur Kutikular-analyse tertiärer Blätter I. *Palaeontographica*, Abt. B, Paläophytol. 91: 7–92.
- KRUTZSCH, W. 1970. Die stratigraphisch verwertbaren Sporen und Pollenformen des mitteleuropäischen Alttertiärs. *Jahrb. Geol. Bot.* 3: 309–379.
- KUPRIANOVA, L. A. 1962. Palynological data and the systematics of the Fagales and Urticales [translated from Russian by J. H. Jones]. Pp. 17–25 in *Soviet Reports From the First International Palynological Conference*. U.S.S.R. Acad. Sci., Moscow. [Examined in abstract form in Ref. *Žurn. Biol.* 18: B139. 1963.]
- . 1967. Palynological data for the history of the Chloranthaceae. *Pollen & Spores* 9: 95–100.
- KVAČEK, Z. & H. WALTHER. 1981. Studium über *Quercus cruciata* Al. Braun und analoge Blattformen aus den Tertiär Europas. *Acta Palaeobot.* 21: 77–100.
- LAMOTTE, R. S. 1952. Catalogue of Cenozoic plants of North America through 1950. *Mem. Geol. Soc. Amer.* 51: 1–381.
- LANGDON, L. D. 1947. The comparative morphology of the Fagaceae I. The genus *Nothofagus*. *Bot. Gaz. (Crawfordsville)* 108: 350–371.
- LAURENT, L. 1912. Flore fossile des Schistes de Menat (Puy-de-Dôme). *Ann. Mus. Natl. Nat., Geol. (Marseille)* 14: 1–246.
- & P. MARTY. 1909. Note sur le *Castanea avernensis* de Menat. *Compt. Rend. Assoc. Franc. Advancem. Sci. (Congr. du Lille, 1909)*: 1–8.
- LAWRENCE, G. H. M. 1951. *Taxonomy of Vascular Plants*. MacMillan Co., New York.
- LEE, C.-S. 1968. Comparative Wood Anatomy of the Fagaceae of Taiwan. M.S. Thesis. Oregon State Univ., Corvallis.
- LESQUEREUX, L. 1859. On some fossil plants of recent formations. *Amer. J. Sci. Arts, Ser. 2*, 27: 359–366.
- . 1874. Contributions to the Fossil Flora of the Western Territories, Part I, The Cretaceous Flora. United States Geological Survey of the Territories, Washington, D.C.
- . 1878. Contributions to the Fossil Flora of the Western Territories, Part II, The Tertiary Flora. United States Geological Survey of the Territories, Washington, D.C.
- LOZANO-C., G., J. HERNÁNDEZ-COMACHO & J. E. HENAO-S. 1979. Hallazgo del género *Trigonobalanus* Forman, 1962 (Fagaceae) en el neotrópico—I. *Caldasia* 12: 517–537.
- LUONG, N.-T. 1965. The boundary between the genera *Castanopsis* and *Lithocarpus* and some data on their taxonomy. *Bot. Žurn. (Moscow & Leningrad)* 50: 997–1001. [In Russian.]
- MACGINITIE, H. D. 1937. The flora of the Weaver-ville Beds of Trinity Co., California. *Publ. Carnegie Inst. Wash.* 465: 83–151.
- . 1941. A Middle Eocene flora from the central Sierra Nevada. *Publ. Carnegie Inst. Wash.* 534: 1–178.

- . 1962. The Kilgore flora: a late Miocene flora from Nebraska. Univ. Calif. Publ. Geol. Sci. 35: 67–158.
- . 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. Univ. Calif. Publ. Geol. Sci. 83: 1–203.
- MAI, D. H. 1964. Die Mastixioideen-Flora im Tertiär der Oberlausitz. Paläontol. Abh., Abt. B, Paläobot. 2: 1–192.
- . 1970. Die tertiären Arten von *Trigonobalanus* Forman (Fagaceae) in Europa. Jahrb. Geol. 3(1967): 381–409.
- MANCHESTER, S. R. 1981a. Fossil plants of the Eocene Clarno Nut Beds. Oregon Geol. 43: 75–81.
- . 1981b. Fossil History of the Juglandaceae. Ph.D. Thesis. Indiana Univ., Bloomington.
- . 1983. Eocene fruits, wood and leaves of the Fagaceae from the Clarno Formation of Oregon. Amer. J. Bot. 70(5, 2): 74. [Abstract.]
- & P. R. CRANE. 1983. Attached leaves, inflorescences and fruits of *Fagopsis*, an extinct genus of fagaceous affinity from the Oligocene Florissant Flora of Colorado, U.S.A. Amer. J. Bot. 70: 1147–1164.
- MASAMUNE, G. & T. TOMIYA. 1948. *Limlia*, a new genus of Fagaceae from Formosa. Acta Bot. Taiwan. 1: 1–3.
- MATSUO, H. 1968. A study of the Neogene plants in the inner side of Central Honshu, Japan. II: on the Minoshirotori Flora (Pliocene) of the paleovolcano-lake deposits. Ann. Sci. (Kanazawa Univ.) 5: 29–77.
- . 1971. Paleogene mega-plant remains of the Tsushima Islands, Japan. Bull. Natl. Sci. Mus. 14: 671–710.
- MELCHIOR, H. 1964. Reihe Fagales. Pp. 44–51 in A. Engler, Syllabus der Pflanzenfamilien, 12th edition, Volume 2. Berlin.
- MENENDEZ, C. A. 1971. Floras Tertiarias de la Argentina. Ameghiniana 8: 357–371.
- & M. A. FILICE. 1975. Las especies de *Nothofagidites* del sedimentos Tertiarios y Cretácicos estancia la sara, norte de Tierra del Fuego, Argentina. Ameghiniana 12: 165–183.
- MENNEGA, A. M. 1980. Wood structure of *Trigonobalanus excelsa* G. Lozano-C., Hdz-C. & Henao (Fagaceae). Caldasia 13: 97–101.
- METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons, Volumes 1–2. Clarendon Press, Oxford.
- & L. CHALK. 1979. Anatomy of the Dicotyledons, 2nd edition, Volume 1. Clarendon Press, Oxford.
- MTCHEDLISHVILI, N. D. 1961. Pollen and spores of western Siberia. Jurassic-Paleocene. Trudy Vsesoyuzn. Neftyanogo Naučno-Issl. Geol.-Razvedochnogo Inst. 177: 329–333.
- MULLER, C. H. 1942a. The problem of genera and subgenera in the oaks. Chron. Bot. 7: 12–14.
- . 1942b. The Central American species of *Quercus*. Misc. Publ. U.S. Dept. Agric. 477: 1–216.
- . 1952. Ecological control of hybridization in *Quercus*: a factor in the mechanism of evolution. Evolution 6: 147–161.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. (Lancaster) 47: 1–145.
- MÜLLER-STOLL, W. R. & E. MADEL. 1957. Über tertiäre Eichenhölzer aus dem pannonischen Becken. Senckenberg. Leth. 38: 121–168.
- NAKAI, T. 1939. *Castanopsis*, *Pasania* and their allies the Japanese Empire. J. Jap. Bot. 15: 185–244, 257–277.
- NATHORST, A. G. 1888. Zur fossilen Flora Japan's. Paläontol. Abh. 4: 197–250.
- NAVALE, G. K. 1964. *Castanoxylon* gen. nov. from Tertiary beds of the Cuddalore Series near Pondicherry, India. Palaeobotanist 11: 131–137.
- NEWBERRY, J. S. 1898. The later extinct floras of North America. Monogr. U.S. Geol. Surv. 35: 1–295.
- NIXON, K. C. 1982. In support of recognition of the family Nothofagaceae Kuprianova. Publ. Bot. Soc. Amer., Misc. Ser. 162: 102. [Abstract.]
- NORRIS, G. & A. D. MIALL. 1984. Arctic biostratigraphic heterochrony. Science 224: 174–175. [Letter.]
- NOTZOLD, T. 1961. Fossil Früchte und Samen aus den Niederlausitzer Braunkohlenrevier. Geologie 10: 231–245.
- OERSTED, A. S. 1871. Bidrag til kundskab om Egefamilien i Nutid og Fortid. Skr. Vidensk.-Selsk., Math.-Naturvidensk. Kl. 9: 333–538.
- OESCH, F. 1969. Low molecular weight carbohydrates and polyols in cambial saps of beech (*Fagus sylvatica* L.) and a number of other deciduous trees. Planta 86: 360–380.
- OGURA, Y. 1949. A fossil wood of *Castanopsis*-type from the Tertiary of Nanano Prefecture. J. Jap. Bot. 24: 15–18.
- OLIVER, W. R. 1925. Biogeographical relations of the New Zealand region. J. Linn. Soc., Bot. 47: 99–139.
- . 1936. The Tertiary Flora of the Kaikorai Valley, Otago, New Zealand. Trans. R. Soc. New Zeal. 66: 289–293.
- ORLANDO, H. 1964. The fossil flora of the surroundings of Ardley Peninsula (Ardley island), 25 de Mayo islands (King George island), South Shetland islands. Pp. 629–636 in Proc. First International Symp. on Antarctic Geol. North Holland Pub. Co., Amsterdam.
- PALMER, E. J. 1948. Hybrid oaks of North America. J. Arnold Arbor. 29: 1–48.
- PENNY, J. S. 1969. Late Cretaceous and early Tertiary palynology. Pp. 331–376 in R. H. Tschudy & R. A. Scott (editors), Aspects of Palynology. Wiley Interscience Publ., New York.
- PETRESCU, I. 1976. Asupra unor lemne de Stejari (*Quercoxylon*) din neogenule de la sud de Cimpulung (Jud. Arges). Univ. Babes-Bolyai din Cluj-Napoca Gradina Botanica, Universitatea, Cluj.
- PHILIPSON, W. R. AND M. N. PHILIPSON. 1979. Leaf veneration in *Nothofagus*. New Zealand J. Bot. 17: 417–421.
- PIEL, K. M. 1971. Palynology of Oligocene sediments from central British Columbia. Canad. J. Bot. 49: 1885–1920.
- PLATEN, P. 1908. Untersuchungen fossiler Hölzer aus dem Westen der Vereinigten Staaten von Nordamerika. Sitzungsber. Naturf. Ges. Leipzig 34: 1–55, 161–164.
- PRAGLOWSKI, J. 1982. Fagaceae L. (Fagoideae). World

- Pollen and Spore Flora 11. Almqvist and Wiksell, Stockholm.
- PRAKASH, U. & E. S. BARGHOORN. 1961a. Miocene fossil woods from the Columbia basalts of central Washington. *J. Arnold Arbor.* 42: 165–193.
- & ———. 1961b. Miocene fossil wood from the Columbia basalts of central Washington. *J. Arnold Arbor.* 42: 347–358.
- PRANTL, K. 1894. Fagaceae. In A. Engler & K. Prantl, *Die Natürlichen Pflanzenfamilien*. Wilhelm Engelmann, Leipzig.
- PREEST, D. S. 1963. A note on the dispersal characteristics of the seeds of the New Zealand podocarps and beeches and their biogeographical significance. Pp. 415–424 in J. L. Gressitt (editor), *Pacific Basin Biogeography*. Bishop Museum Press, Honolulu.
- PRIVE, C. 1975. Étude de quelques bois de chênes tertiaires du Massif Central, France. *Palaeontographica*, Abt. B, Paläophytol. 153: 119–140.
- PURI, G. S. 1965. Some plant microfossils from Nigeria. Pp. 391–404 in G. J. Snowball (editor), *Proceedings of the Central African Scientific and Medical Congress (1963)*, Lusaka, Zambia. Pergamon Press, Oxford and New York.
- RAGONESE, A. M. 1977. *Nothofagoxylon menendezii*, leño petrificado del Terciario de General Roca, Rio Negro, Argentina. *Ameghiniana* 14: 75–86.
- . 1981. Anatomia foliar de las especies sudamericanas de *Nothofagus* Bl. (Fagaceae). *Darwiniana* 23: 587–603.
- RAMANUJAM, C. G. 1966. Palynology of the Miocene lignites from South Arcot district, Madras, Spain. *Pollen & Spores* 8: 149–203.
- RANIECKA-BOBROWSKA, J. 1962. Trzeciorzędowa flora z Osieczowa nad Kwisą (Dolny Śląsk). *Prace Inst. Geol.* 30: 81–223.
- RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- RAY, J. 1682. *Methodus Plantarum Nova*. Faithorne & Kersey, London.
- . 1703. *Methodus Plantarum Emendata et Aucta*. Smith & Walford, London.
- REECE, P. C. 1938. Morphology of the Flowers and Inflorescences of the Fagaceae. Ph.D. Thesis. Cornell Univ., Ithaca, New York.
- ROMER, A. S. 1966. *Vertebrate Paleontology*, 3rd edition. Univ. of Chicago Press, Chicago.
- ROMERO, E. J. 1973. Polen fósil de *Nothofagus* (*Nothofagidites*) del Cretacio y Paleoceno de Patagonia. *Revista Mus. La Plata, Secc. Paleontol.*, n.s. 7: 291–303.
- . 1977. Polen de Gimnospermas y Fagaceas de la Formación Rio Turbio (Eoceno), Santa Cruz, Argentina. FECIC Editorial, Buenos Aires.
- . 1980. Arquitectura foliar de las especies sudamericanas de *Nothofagus* Bl. *Bol. Soc. Argent. Bot.* 19: 289–308.
- & A. C. AGUIRRE. 1982. Arquitectura foliar de las especies de *Nothofagus* (Fagaceae) de Nueva Guinea y Nueva Caledonia. *Bol. Soc. Argent. Bot.* 21: 213–245.
- ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27: 159–188.
- ROUSE, G. E., W. S. HOPKINS & K. M. PIEL. 1971. Palynology of some late Cretaceous and early Tertiary deposits in British Columbia and adjacent Alberta. *Special Pap. Geol. Soc. Amer.* 127: 213–246.
- RÜFFLE, L. 1978. Evolutionary and ecological trends in Cretaceous floras particularly in some Fagaceae. *Cour. Forsch.-Inst. Senckenberg.* 30: 77–83.
- . 1980. Wachstums-Modus und Blatt-Morphologie bei alttertiumlichen Fagales und Hamamelidales der Kreide und der Gegenwart. Pp. 329–341 in *100 Jahre Arbor, 1879–1979*. Berlin.
- & H. KNAPPE. 1977. Entwicklungsgeschichtliche und ökologische Aspekte zur Oberkreide-Flora, besonders einiger Fagaceae. (Hamamelididae). *Z. Geol. Wiss. (Berlin)* 5: 269–303.
- SALARD, M. 1961. Contribution a l'étude paleoxylologique de la Patagonie II. *Rev. Gén. Bot.* 68: 234–270.
- SAPORTA, G. & A. F. MARION. 1878. Révision de la flore Heersienne de Gelinden. *Mém. Acad. Roy. Sci. Belgique* 41: 1–112.
- SCHALKE, H. J. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa). *Scripta Geol.* 15: 1–57.
- SCHIMPER, W. P. 1870–1872. *Traité de Paleontologie Végétale ou la Flore du Monde Primitif*, Volume 2. J. B. Baillière et Fils, Paris.
- SCHOTTKY, E. 1912. Die Eichen des extratropischen Ostasiens und ihre pflanzengeographische Bedeutung. *Bot. Jahrb. Syst.* 47: 617–708.
- SCHUSTER, J. 1908. Über ein pliocänes Eichenholz aus Idaho. *Neues Jahrb. Mineral. Geol. Palaeontol.* 1908: 49–54.
- SCHUSTER, R. M. 1972. Continental movements, "Wallace's Line" and Indomalayan-Australasian dispersal of land plants: some eclectic concepts. *Bot. Rev. (Lancaster)* 38: 1–86.
- . 1976. Plate tectonics and angiosperm origin and dispersal. Pp. 48–138 in C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York.
- SCHWARZ, O. 1936a. Entwurf zu einem natürlichen System der Cupuliferen und der Gattung *Quercus* L. *Notizbl. Bot. Gart. Berlin-Dahlem* 8: 1–22.
- . 1936b. Über die Typologie der Eichenblätter und ihre Anwendung in der Palaobotanik. *Repert. Spec. Nov. Regni Veg. Beih.* 86: 60–70.
- SEIN, M. K. 1961. *Nothofagus* pollen in the London Clay. *Nature* 190: 1030–1031.
- SELMEIER, A. 1970a. Ein *Castanopsis*-Hölz aus jungtertiären Schichten Südbayerns (Schrobenhausen). *Neues Jahrb. Geol. Palaontol. Monatsh.* 1970(4): 235–250.
- . 1970b. *Castanopsis*-Hölzer aus obermiozänen Glimmersanden der südlichen Franckenalb. *Mitt. Bayer. Staatssamml. Palaontol. Hist. Geol.* 10: 309–320.
- . 1970c. *Castanoxylon bavaricum* n. sp. aus jungtertiären Schichten Nordost-Bayerns (Basaltbruch Weidersberg). *Geol. Blätt. Nordost-Bayern* 20: 17–38.
- . 1971. Ein verkieseltes Eichen hölz aus jungtertiären Schichten Niederbayerns (Aidenbach). *Mitt. Bayer. Staatssamml. Palaontol. Hist. Geol.* 11: 205–222.
- . 1972. Ein *Castanopsis*-Hölz aus oberchat-tischen Steigbach-schichten des Allgaus. *Mitt.*

- Bayer. Staatssamml. Palaontol. Hist. Geol. 12: 97–104.
- SHEFFY, M. J. 1972. A Study of the Myricaceae From Eocene Sediments of Southeastern North America. Ph.D. Thesis. Indiana Univ., Bloomington.
- SHIMAJI, K. 1962. Anatomical studies on the phylogenetic interrelationships of the genera in the Fagaceae. Bull. Tokyo Univ. Forest 57: 1–64.
- SIMPSON, G. G. 1953. The Major Features of Evolution. Simon & Schuster Co., New York.
- SITAR, V. 1974. Die fossile Flora Sarmatischer Sedimente aus der Umgebung von Mociar in der mittleren Slowakei. Acta Geol. Geogr. Univ. Comeniana 26: 5–85.
- SMILEY, C. J. & L. M. HUGGINS. 1981. *Pseudofagus idahoensis* N. gen. et sp. (Fagaceae) from the Miocene Clarkia Flora of Idaho. Amer. J. Bot. 68: 741–761.
- SMITH, A. G. & J. C. BRIDEN. 1977. Mesozoic and Cenozoic Paleogeographical Maps. Cambridge Univ. Press, New York.
- SOEPADMO, E. 1968a. Florae Malesianae Praecursores XLVII. Census of Malesian *Castanopsis* (Fagaceae). Reinwardtia 7: 383–410.
- . 1968b. A revision of the genus *Quercus* L. Subgen. *Cyclobalanopsis* (Oersted) Schneider in Malesia. Gard. Bull. Straits Settlements 22: 355–427.
- . 1970. Florae Malesianae Praecursores XLIX. Malesian species of *Lithocarpus* Bl. (Fagaceae). Reinwardtia 8: 197–308.
- . 1972. Fagaceae. Fl. Males. I, 7: 265–403.
- SRIVASTAVA, S. K. 1969. Assorted angiosperm pollen from the Edmonton Formation (Maestrichtian), Alberta, Canada. Canad. J. Bot. 47: 975–989.
- STACE, C. A. 1965. Cuticular studies as an aid to plant taxonomy. Bull. Brit. Mus. (Nat. Hist.), Bot. 4: 1–78.
- STEBBINS, G. L., E. B. MATZKE & C. EPLING. 1947. Hybridization in a population of *Q. marilandica* and *Q. ilicifolia*. Evolution 1: 79–88.
- STERN, W. L. 1973. Development of the amentiferous concept. Brittonia 25: 316–333.
- STOPE, M. C. & K. FUJI. 1910. Studies on the structure and affinities of Cretaceous plants. Phil. Trans., Ser. B, 201: 1–90.
- STOVER, L. E. & P. R. EVANS. 1973. Upper Cretaceous-Eocene spore pollen zonation, offshore Gippsland Basin, Australia. Geol. Soc. Austral. Special Publ. 4: 55–72.
- SZAFER, W. 1961. Miocene flora from Stare Gliwice in upper Silesia. Prace Inst. Geol. 33: 1–205.
- TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Oliver and Boyd, Edinburgh.
- . 1982. Fagaceae. Pp. 60–120 in Flowering Plants of the USSR, Volume 2, Nauka, Leningrad.
- TANAI, T. 1961. Neogene floral change in Japan. J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 1: 119–398.
- . 1967. Tertiary floral changes of Japan. Pp. 317–334 in Jubilee Publ. Commemorating Prof. Sasa's 60th birthday.
- . 1970. The Oligocene floras from the Kushiro Coal Field, Hokkaido, Japan. J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 14: 383–514.
- . 1974. Evolutionary trend of the genus *Fagus* around the Northern Pacific Basin. In Symposium on Origin and Phytogeography of Angiosperms. Birbal Sahni Inst. Paleobot. Special Publ. 1: 62–83.
- & K. HUZIOKA. 1967. Climatic implications of Tertiary floras in Japan. Pp. 89–94 in K. Hatai (editor), Tertiary Correlations and Climatic Changes in the Pacific. Eleventh Pacific Science Congress (1966), Tokyo.
- & T. ONOE. 1961. A Mio-Pliocene flora from the Ningyo-Toge area on the border between Tottari and Okayama Prefectures, Japan. Rep. Geol. Surv. Japan 187: 1–63.
- & N. SUZUKI. 1965. Late Tertiary floras from northeastern Hokkaido, Japan. Special Pap. Palaeontol. Soc. Japan 10: 1–117.
- & A. YOKOYAMA. 1975. On the lobed oak leaves from the Miocene Kobe Group, western Honshu, Japan. J. Fac. Sci. Hokkaido Imp. Univ., Ser. 4, Geol. 17: 129–141.
- THOMPSON, P. M. & R. H. MOHLENBROCK. 1979. Foliar trichomes of *Quercus* subgenus *Quercus* in the eastern United States. J. Arnold Arbor. 60: 350–366.
- TIFFNEY, B. H. 1984 [1985]. Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. Ann. Missouri Bot. Gard. 71: 551–576.
- TRALAU, H. 1962. Die Spättertiären *Fagus* Arten Europas. Bot. Not. 115: 147–176.
- TRELEASE, W. 1917. Naming American hybrid oaks. Proc. Amer. Philos. Soc. 56: 44–52.
- . 1918. The ancient oaks of America. Mem. Brooklyn Bot. Gard. 1: 492–501.
- . 1924. The American oaks. Mem. Natl. Acad. Sci. 20: 1–255.
- TUCKER, J. M. 1974. Patterns of parallel evolution of leaf forms in new world oaks. Taxon 23: 129–154.
- TUCKER, J. M., W. E. SUNDAHL & D. O. HALL. 1969. A mutant *Lithocarpus densiflorus*. Madroño 24: 221–225.
- UNGER, F. 1850. Genera et Species Plantarum Fossilium. Wilhelm Braumüller, Vindobonae.
- VAN DER BURGH, J. 1973. Hölzer der neiderrheinischen Braunkohlenformation, 2. Hölzer der Braunkohlengruben "Maria Theresia: zu Herzogenrath "Zukunft West" zu eschweiler und "Victor" (Zülpich Mitte) zu Zülpich. Nebst einer systematisch-anatomischen Bearbeitung der Gattung *Pinus* L. Rev. Paleobot. Palynol. 15: 73–275.
- . 1978a. The Pliocene flora of Fortuna-Garsdorf I. Fruits and seeds of Angiosperms. Rev. Palaeobot. Palynol. 26: 173–211.
- . 1978b. Hölzer aus dem Pliozän der Niederrheinischen Bucht. Fortschr. Geol. Rheinl. Westfalen 28: 213–275.
- VAN STEENIS, C. G. 1953. Results of the Archbold Expeditions Papuan *Nothofagus*. J. Arnold Arbor. 34: 300–374.
- . 1971a. *Nothofagus*, key genus of plant geography, in time and space, living and fossil, ecology and phylogeny. Blumea 19: 65–98.
- . 1971b. Revision of *Nothofagus* in New Caledonia. Adansonia, Ser. 2, 11: 615–624.
- VAN VALEN, L. 1976. Ecological species, multispecies, and oaks. Taxon 25: 233–239.
- VATER, H. 1884. Die fossilen Hölzer der Phosphor-

itlager des Herzogthums Braunschweig. Z. Deutsch. Geol. Ges. 36: 783–853.

WARD, L. F. 1905. Status of the Mesozoic floras of the United States. U.S. Geol. Surv. Pap. 2: 1–616.

WHEELER, E. F., R. A. SCOTT & E. S. BARGHOORN. 1978. Fossil dicotyledonous woods from Yellowstone National Park, II. J. Arnold Arbor. 59: 1–26.

WINKLER, H. 1904. Betulaceae. In A. Engler, Das Pflanzenreich, Volume 19. Wilhelm Engelmann, Berlin.

WILLIS, J. C. 1973. A Dictionary of the Flowering Plants and Ferns, 8th edition. Cambridge Univ. Press, Cambridge.

WOLFE, J. A. 1968. Paleogene biostratigraphy of non-marine rocks in King County, Washington. Profess. Pap. U.S. Geol. Surv. 571: 1–33.

———. 1973. Fossil forms of Amentiferae. Brittonia 25: 334–355.

———. 1977. Paleogene floras from the Gulf of Alaska Region. Profess. Pap. U.S. Geol. Surv. 997: 1–108.

ZASTAWNIAK, E. 1981. Tertiary leaf flora from the Point Hennequin Group of King George Island (South Shetland Islands, Antarctica). Preliminary Report. Stud. Geol. Polon. 72: 97–108.

APPENDIX I

A FOLIAR “KEY” FOR CONFIRMING FAGACEOUS AFFINITIES AMONG MEMBERS OF THE
HAMAMELIDOPSIDAE (AMENTIFERAЕ)

The following “key” is designed to help confirm the identity of fagaceous leaves among similar forms in the Hamamelidopsidae sensu Cronquist (1981). It is based on broad summary publications (e.g., Lawrence, 1951; Metcalf & Chalk, 1950, 1979; Hutchinson, 1967; Willis, 1973; Cronquist, 1981), familial surveys (e.g., Winkler, 1904; Sheffy, 1972), personal communications with those working with amentiferous leaves, and personal observations.

- 1. Stomata anomocytic or cyclocytic 2
- 1. Stomata neither anomocytic nor cyclocytic
 - Balanopaceae
 - Barbeyaceae
 - Casuarinaceae
 - Cercropiaceae
 - Daphniphyllaceae
 - Hamamelidaceae
 - Moraceae pro parte
 - Platanaceae pro parte
 - Tetracentraceae
 - Trochodendraceae
 - Ulmaceae pro parte
 - Urticaceae pro parte
- 2. Leaves simple 3
- 2. Leaves compound
 - Cannabidaceae pro parte
 - Juglandaceae
 - Moraceae pro parte
 - Rhoipteliaceae
- 3. Leaves with pinnate venation 4
- 3. Leaves with distinctly acrodromous or flabellate venation
 - Cannabidaceae pro parte
 - Cercidophyllaceae
 - Moraceae pro parte
 - Myrothamnaceae
 - Platanaceae pro parte
- 4. Leaves, when toothed, possessing craspedodromous secondary veins 5
- 4. Leaves toothed without purely craspedodromous secondary veins
 - Eucommiaceae
 - Platanaceae pro parte
- 5. Leaves lacking anastomosing, fibrous, fine venation and strong marginal veins; areolation well developed consisting of small orthogonal, nearly isodiametric units 6
- 5. Leaves possessing anastomosing, fibrous, fine venation; strong marginal veins and elongate areoles
 - Didymelaceae
- 6. Leaves, when toothed, possessing less than two teeth per secondary over more than half of the leaf length; or as in some *Nothofagus* species, with more than two teeth per secondary over more than two-thirds of the leaf length and always possessing simple unicellular (type 1) trichomes and often large glands (type 17) 7
- 6. Leaves serrate with more than two irregularly spaced teeth per secondary; trichomes restricted to uniseriate nonglandular forms
 - Eupteliaceae
- 7. Leaves usually bearing symmetrical bases; epidermal idioblasts absent; types 1 and 2 trichomes, when present, lack hooks; type 3 trichomes, when present, possess unicellular bases; epidermis neither calcified nor silicified 8

7. Leaves frequently with markedly asymmetrical bases; idioblasts (e.g., Lithocysts) common in the upper epidermis; short unicellular trichomes (types 1 and 2) common and often hooked; type 3 trichomes when present are borne on multicellular bases; epidermis frequently calcified or silicified Cannabidaceae pro parte
..... Moraceae pro parte
..... Ulmaceae pro parte
..... Urticaceae pro parte
8. Thick-walled type 1 trichomes, when present unicellular 9
8. Trichomes resembling type 1 always multicellular with thin cross septae Leitneriaceae
9. Leaves neither linear-oblong and pinnatifid with semicordate stipules, nor spatulate with prominent looping secondaries; glandular scales, when present, subtended by simple trichome bases 10
9. Leaves with glandular scales subtended by bicellular (rarely tri- or tetra-cellular) bases, or when absent, leaves linear-oblong and pinnatifid with semicordate stipules, or leaves spatulate with prominent looping secondaries Myricaceae
10. Leaves rarely doubly serrate; when doubly serrate, serrate over more than two-thirds of the lamina length possessing only types 1, 2 and often type 17 trichomes Fagaceae
10. Leaves nearly always doubly serrate possessing modified and/or uniseriate multicellular trichomes and/or glandular trichomes in addition to types 1 and 2 Betulaceae

APPENDIX II

KEY TO THE GENERA OF FAGACEAE (BASED ON FOLIAR FEATURES)

1. Leaves lobed 2
1. Leaves not lobed 4
2. Upper cuticles revealing sinuate anticlinal walls; may possess only trichome types 1 and 15, never tufts *Fagus* (some cultivars)
2. Upper cuticles revealing straight to slightly curved anticlinal walls; may possess a variety of trichome types including tufts of various sorts 3
3. Lobes nearly always pointed and aristate *Quercus* (sect. *Erythrobalanus* pro parte)
3. Lobes rounded and nonaristate *Quercus* [sects. *Erythrobalanus* (rare), *Lepidobalanus*, *Mesobalanus*, and *Cerris* pro parte]
4. Leaves bearing persistent yellowish, peltate (type 11) trichomes *Chrysopsis*
4. Leaves not bearing persistent yellowish, peltate (type 11) trichomes 5
5. Leaves usually bearing large globular (type 17) trichomes, or curly thin-walled (type 12) trichomes forming a dense cover over the lower surface of the leaf and/or type 2 trichomes common over major veins; all leaves lacking tufts; teeth, when present, compound or biconvex (type A1) *Nothofagus*
5. Leaves never bearing type 17 trichomes; teeth nearly always simple; type 2 trichomes not abundant and when present usually restricted to the midrib or petiole; type 12 trichomes rare and never forming a dense mat 6
6. Upper cuticles of mature leaves revealing sinuous anticlinal walls; secondary veins strictly craspedodromous and very straight except near the base of the leaf where they often recurve; trichomes restricted to types 1, 15 and rarely 2 *Fagus* pro parte (all except lobed cultivars)
6. Upper cuticles of mature leaves generally lacking sinuous anticlinal walls; secondary veins craspedodromous or camptodromous usually slightly curved, or less regular and straight; trichomes usually include tufts in addition to or instead of trichome types 1 and 15 7
7. Lower cuticles bearing appressed parallel (type 9) trichomes *Lithocarpus* pro parte
7. Lower cuticles without type 9 trichomes 8
8. Leaves strictly craspedodromous, lacking intersecondary veins; secondary veins regular and straight to slightly curved; teeth regularly spaced 9
8. Leaves camptodromous or craspedodromous with irregularly spaced secondaries; intersecondaries often present 14
9. Teeth not rounded and often spinose 10
9. Teeth rounded and fairly coarse *Quercus* (sects. *Lepidobalanus*, *Mesobalanus*, and *Cerris* pro parte)
10. Leaves lacking large multiradiate (type 10) trichomes 11
10. Leaves bearing large type 10 trichomes *Lithocarpus* (*L. densiflorus* only)

11. Leaves with abundant thin-walled peltate (type 13) trichomes, with darkly staining bases, on the lower surface *Castanopsis* pro parte
11. Leaves lacking type 13 trichomes 12
 12. Leaves lanceolate, subcoriaceous, nearly glabrous at maturity with only simple trichome bases widely scattered on the epidermis; upper cuticles with sinuate anticlinal walls 13
 12. Leaves chartaceous (rarely subcoriaceous) bearing at least the proximal portions of simple uniseriate (type 15) and/or capitate (type 16) trichomes; tufts (types 5 and 6) usually present and often abundant; upper cuticle revealing straight to rounded anticlinal walls *Quercus* (sects. *Cerris*, *Cyclobalanopsis*, *Erythrobalanus*, *Lepidobalanus*, and *Macrobalanus* pro parte *Castanea*)
13. Leaves with greater than 11 pairs of secondary veins *Lithocarpus* pro parte (*L. cornea*)
13. Leaves with fewer than 11 pairs of secondary veins *Quercus* (sect. *Cyclobalanopsis* pro parte)
 14. Leaves holly-like, coriaceous to sclerophyllous secondaries usually irregularly spaced, often entering large spinose teeth *Quercus* (sects. *Erythrobalanus* pro parte, *Lepidobalanus* pro parte, and *Protobalanus*)
 14. Leaves entire or partially toothed, not holly-like 15
 15. Leaves entire or toothed only near the apex; apex caudate or attenuate (rarely, simply acute), often forming a drip tip 16
 15. Leaves entire or with irregularly spaced bristle bearing teeth; apex not caudate and not bearing a drip tip 17
 16. Lower cuticle speckled with darkly staining thin-walled peltate (type 13) trichome bases; type 13 trichomes often present in abundance *Castanopsis* pro parte
 16. Lower cuticle lacking type 13 trichomes; darkly staining bases, when present, subtending one or more of trichome types 15, 16, and 17 *Quercus* (sect. *Cyclobalanopsis* pro parte) *Lithocarpus* pro parte
 17. Leaves entire-margined, sclerophyllous; with large multiradiate (type 10) trichomes *Lithocarpus* (entire-margined *L. densiflorus*)
 17. Leaves not bearing type 10 trichomes 18
 18. Leaves possessing "glandular" peltate (type 19) trichomes or thin uniseriate (type 15) trichomes with very broad, darkly staining, basal cells (Jones, 1984, pl. 52D) or secondary veins that end nearly in the sinus above the teeth, as in Jones (1984, pl. 14A, B, D) *Trigonobalanus*
 18. Leaves without any of the above characteristics *Quercus* (sects. *Erythrobalanus*, *Lepidobalanus*, and *Macrobalanus* pro parte)

APPENDIX III

CLASSIFICATION OF TRICHOMES
OF THE FAGACEAE

Trichomes have been used taxonomically in parts of the Fagaceae for many years (Dyal, 1936; Hardin, 1975, 1979; Thomson & Mohlenbrock, 1979), yet no one has adequately surveyed the trichomes in the entire family. Camus (1934–1954) provided a truly remarkable analysis but she did not investigate the Fagoideae and her data from the Castaneoideae and Quercoideae is lost in a sea of other morphological and anatomical data. Like most neobotanists, she tailored her work for use on modern plants and neglected some of the less taxonomically useful features upon which paleobotanists must often rely. Her study is undoubtedly the most complete, but she failed to thoroughly classify and interpret the trichomes she observed. Hardin (1976) provided a good analysis in his series of papers on the trichomes of *Quercus* species from the southeastern United States, however, the taxonomic scope of this work is fairly limited. The following is an attempt to classify and describe the major trichome types found

among all extant Fagaceae. This classification is built historically on those of Camus, Dyal, Hardin, and others. The classification must be arbitrary in many respects because most forms intergrade with at least one other type and discrete boundaries usually do not exist. I have attempted to combine forms that cannot be distinguished without sectioning or other time consuming methods. All types listed here can be identified through examination of whole leaf material with a standard light microscope or a scanning electron microscope. I have divided the trichome types into three major groups; nonglandular, intermediate, and glandular. As in the classification schemes of earlier authors, the terms glandular and nonglandular are not strictly correlated with the functions they imply. They are, rather, terms that roughly describe the apparent function of the trichome types. Each term is associated with a syndrome or combination of characteristics under the lettered headings below.

A. "Nonglandular" trichomes. Trichomes of this group are generally thick-walled, apparently nonglan-

dular, and unicellular or composed of unicellular elements. The function of these trichomes appears to be related to physical protection or "covering." This class corresponds fairly well to the "poils tecteurs" of Camus (1928–1929, 1934–1954).

Type 1 (solitary unicellular). Trichomes of this type are usually thick-walled, fairly long, and straight to slightly wavy in course (Fig. 1). In those species in which they occur on fine veins, they are usually erect, bristle-like, and relatively short (Fig. 2). When restricted to the petiole, midrib, and other major veins, these trichomes tend to be longer and somewhat appressed to the vein from which they arise. These long appressed forms are usually thinner walled and frequently occur in young leaves. They are not as resistant as the short erect ones and tend to be lost with time. This rather fragile form conforms to "poils tecteurs unicellules courbés à la base" of Camus (1934–1954, volume III). Trichome type 1 is perhaps the most widely dispersed trichome type in the Fagaceae and is found in all genera (see Table 2). This trichome type appears to form one end of a continuum from solitary unicellular trichomes to the many element type 6 tufts. Type 1 trichomes are most abundant and reach their highest development in *Fagus* and some *Nothofagus*, in which they cover the major veins and margins of young leaves (Fig. 3). Many of these trichomes are lost as the leaf ages, but a few usually can be found in protected areas on or near the midrib. This trichome type corresponds to "poils tecteurs (unicellulaires) isolés" of Camus (1928–1929, 1934–1954) and "solitary" of Hardin (1976).

Type 2 (unicellular conical). Trichomes of this type are short, thick-walled, and erect (Fig. 4). They are generally restricted to the major veins as well. Some, particularly in *Nothofagus*, have a distinctive, darkly staining, broad basal portion (thickened foot cell of Hill, 1983a) (Fig. 5). There is essentially no difference between types 1 and 2 trichomes other than length. Yet, the taxonomic distribution of these short trichomes and their resultant systematic utility justify their separation into a distinct type. This trichome type is best developed in the genus *Nothofagus* and is rare outside the Fagoideae sensu lato.

Type 3 (papillae). Papillae are included here, though straining application of the term trichome, because they intergrade with broad-based type 2 trichomes. They are relatively rare in the Fagaceae, occurring only in a few species of *Quercus* and *Lithocarpus* and one species of *Nothofagus*. When present they adorn nearly all otherwise undifferentiated lower epidermal cells (Figs. 6, 7) except in *N. obliqua*, in which they are restricted to the adjacent epidermal cells of stomatal complexes. They are thick-walled and arise from normal-sized epidermal cells.

Type 4 (appressed laterally attached unicellular). These trichomes resemble type 1 except that they are attached laterally and are generally thin-walled. It is often difficult to determine the point of attachment using standard methods of examination. Camus (1934–1954) illustrated a number of these from young leaves (Fig. 8). They are exceedingly rare on mature leaves, where they are confined to the larger veins. Their presence appears to be restricted to the genus *Quercus*. These correspond to the "poils unicellulaires apprimés,

en navette" of Camus (1934–1954) and "appressed laterals" of Hardin (1976).

Type 5 (fasciculate). These "nonglandular" trichomes are characterized by the possession of two or more (generally four to seven) unicellular, thick-walled elements joined together only at the base. The elements may be erect and travel parallel to each other, forming a closed tuft (Fig. 9), or they may splay out to varying degrees (Fig. 10) eventually to intergrade with stellate forms. Those with very long elements often intertwine (Fig. 11). Fasciculate tufts occur in a sessile form that is usually associated with radially septate bases, and a pedicellate form, in which there is a very short epidermal pedestal upon which the rays are borne. Fasciculate tufts are found in greater abundance near major veins in most mature leaves but may form a dense cover, in some species, obscuring the entire lower leaf surface. Like most, trichomes of this type are much more common and longer on the lower leaf surface. This trichome type is restricted to the Castaneoideae and Quercoideae. It reaches its greatest development in the genus *Quercus*. This type corresponds to some of Camus' (1928–1929, 1934–1954) "poils fascicules en bouquets ou buissons, articulés libres." However, Camus included types 8, 10, and 14 in this broad group as well. Hardin's (1976) "fasciculate" included those assigned to this group plus those of type 8, which he considered to be a subtype.

Type 6 (stellate). Stellate trichomes consist of three or more "nonglandular," unicellular, and generally thick-walled elements that radiate from a common point of attachment in a fashion parallel, or nearly parallel, to the leaf surface (Fig. 12). These trichomes are usually smaller than erect tufts, which may occur on the same leaf. They frequently can be distinguished from "open" forms of type 5 trichomes by the prominent pie-shaped wedges produced at the juncture of the constituent elements (Figs. 13, 14). Two forms of this trichome have been observed. Elements of the more common form occupy a common plane. The second form is bilayered and contains a second set of elements in a plane above the first (Fig. 15). Stellate trichomes, when abundant, are scattered evenly over the fine venation of the lower surface. They rarely occur on the upper surface. They are usually restricted to large veins or sometimes only the petiole, particularly in specimens where they are rare. They are present in both the Castaneoideae and Quercoideae and reach their greatest development in *Quercus* and *Castanea*. These conform directly to Hardin's (1976) "stellate" type except that it includes bilayered forms that according to his classification would be multiradiate. Camus (1934–1954) used the term "poils étioles" for these although some of those she classified as "poils fascicule's" are included here.

Type 7 (fused stellate). Fused stellate trichomes resemble the above except that the rays are fused for a significant portion of their length. They are fused beyond the tapered portion of the basal union (Figs. 16, 17). They generally possess a larger number of elements than type 6 (sometimes as many as 18). These are common only in *Quercus* and reach their greatest development in subsection *Virentes* of the white oak group. They are most commonly found distributed over the lower surface of the leaf. Plants that bear fused stellate trichomes usually inhabit warm coastal environments where windy conditions and sandy soil prevail. This

is equivalent to Hardin's (1976) type of the same name. Camus did not distinguish trichomes of this type from other stellate forms.

Type 8 (stipitate fasciculate). Stipitate fasciculate trichomes are similar to type 5 except that the cells are fused well beyond the base (Fig. 18). They intergrade with type 5, but differences in their taxonomic and physical distributions warrant recognition as a separate type. They are usually found in the angles of the secondary veins on the lower sides of the leaves. However, they are scattered over the fine veins as well in a few specimens (Fig. 19). In some cases the elements are extremely long and intertwine (Fig. 20). They are found only in *Quercus* and, rarely, *Lithocarpus*. They reach their maximum development in *Quercus* section *Erythrobalanus*. Sessile forms have been observed but most are pedicellate (Fig. 21). Hardin (1976) considered this a subtype of "fasciculate" trichomes.

Type 9 (appressed parallel tuft). This "nonglandular" trichome type consists of two or more generally thick-walled, unicellular elements that are nearly coplanar and approximately parallel with the leaf surface and each other (Fig. 22). The bases of the elements form a linear band rather than a rounded mass (Fig. 23). They are restricted, with few exceptions, to *Lithocarpus*, where they occur in nearly all specimens. They are one of the salient characteristics of *Lithocarpus* leaves. Camus (1934–1954) classified these trichomes under the category "poils en doigts de gant" or hairs like fingers of a glove.

Type 10 (multiradiate). These "nonglandular" trichomes are composed of several (ca. eight), unicellular, generally thick-walled, elements that emerge in a variety of seemingly random directions from a typically rounded common base (Fig. 24). These are usually found distributed over the lower surface of the lamina.

This type is generally restricted to the genus *Quercus* but a particularly large and impressive form is found on leaves of *L. densiflorus* (Figs. 25, 26). This is the only occurrence, outside of *Quercus*, noted in this study. Camus (1934–1954) included the *L. densiflorus* form in her "poils étioles." Hardin (1976) included these in a group of the same name.

B. Intermediate trichomes. Trichomes assigned to this group consistently show a combination of the characteristics of "glandular" and "nonglandular" forms.

Type 11 ("thick"-walled peltate). These trichomes consist of a uniseriate stalk, which bears a somewhat circular cap of radially fused, relatively thick-walled cells. These trichomes are most often yellowish and cover the entire lower epidermis (Figs. 27–29). Although many are lost with age, they are abundant even in mature leaves. These scales are unique to, and characteristic of, the genus *Chrysolepis*. They are similar to type 13 trichomes (Fig. 33) but differ in a number of ways: they are smaller (average radius ca. 100 μm versus 180 μm), have thicker cell walls, contain yellowish resinous material, and perhaps most importantly, the cellular components of the cap tend to be radially fused (Fig. 27), which is not the case in those of type 13 (Fig. 33). Camus (1928–1929) included this in her "poils écailléux."

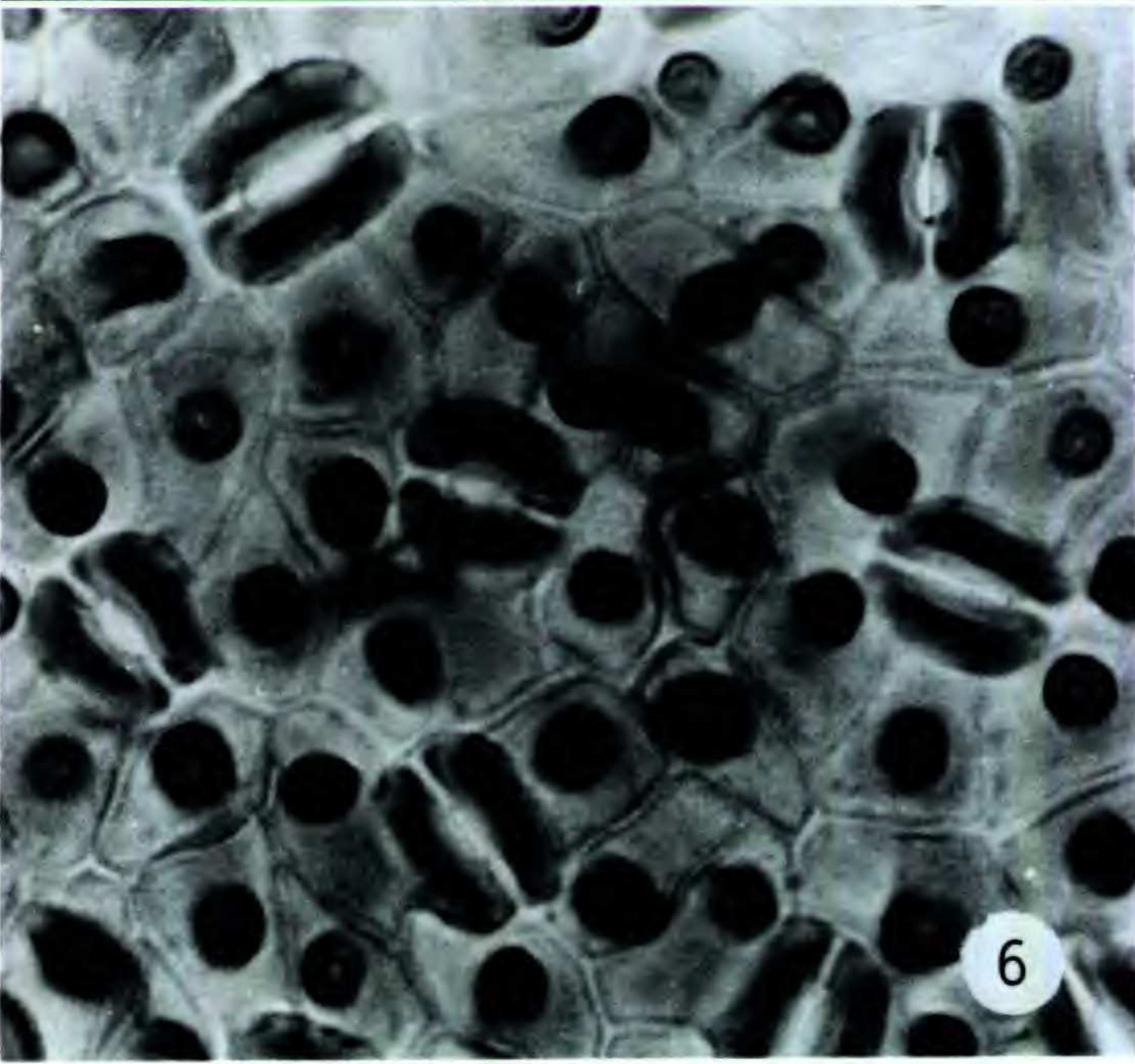
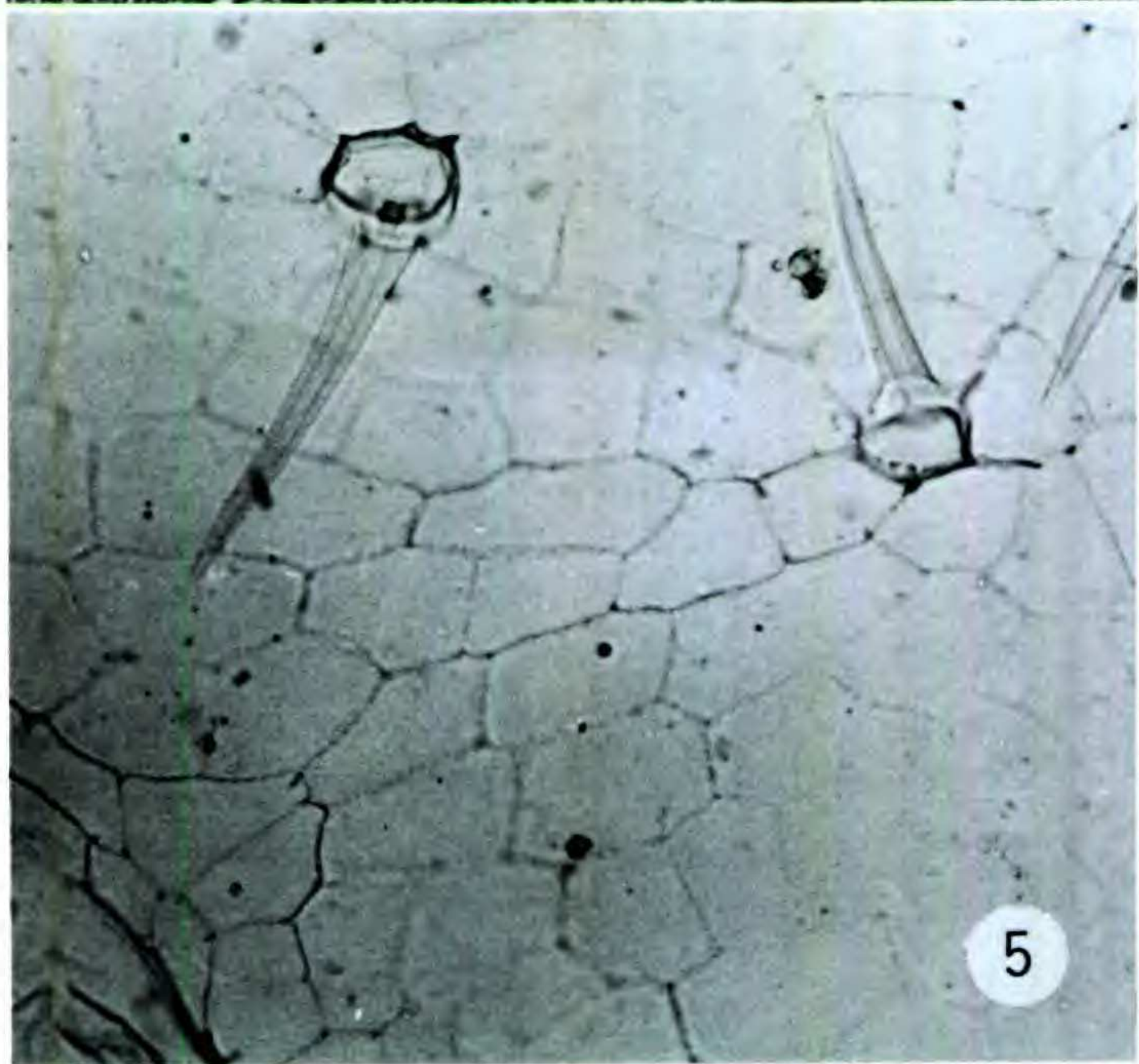
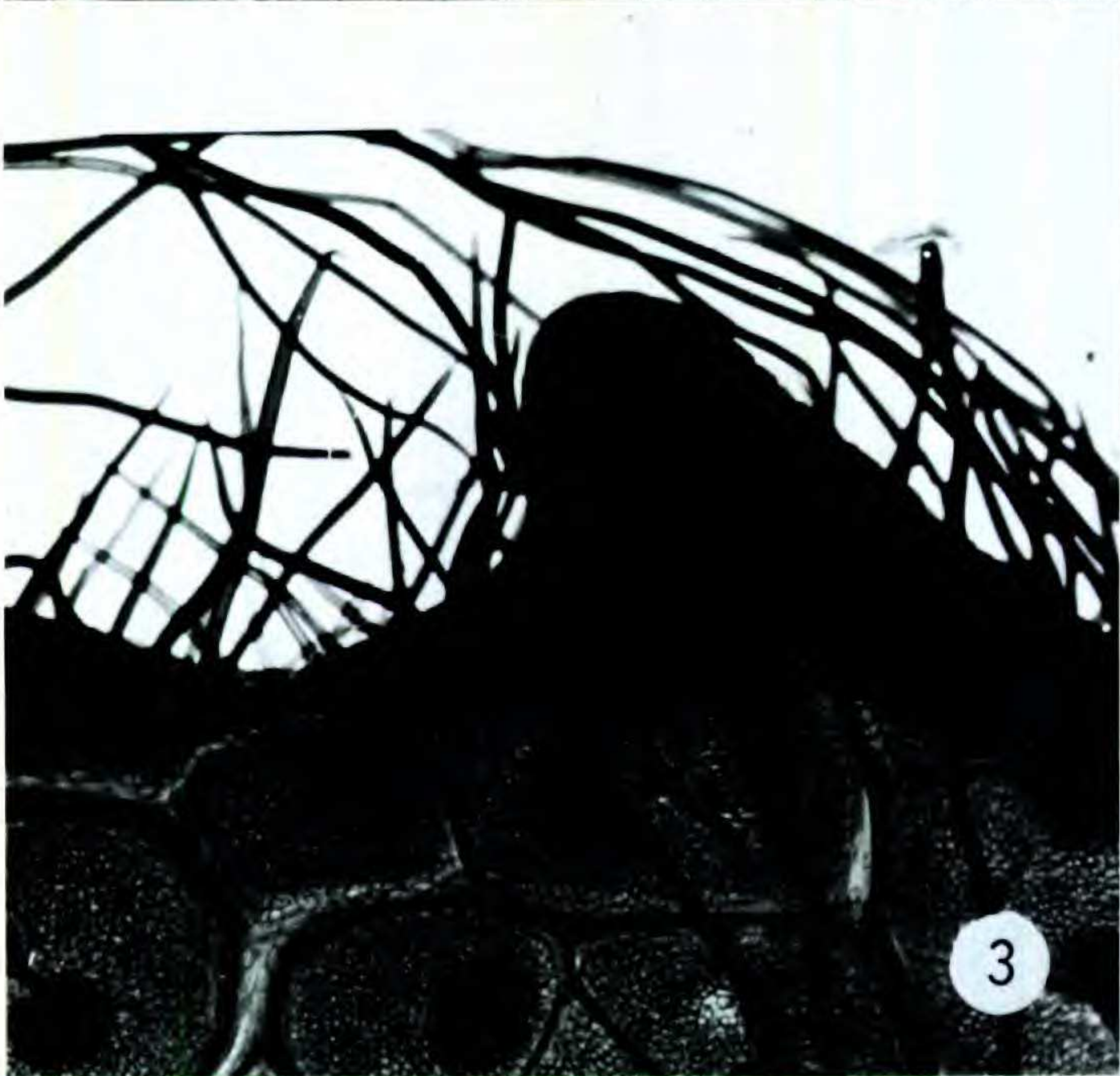
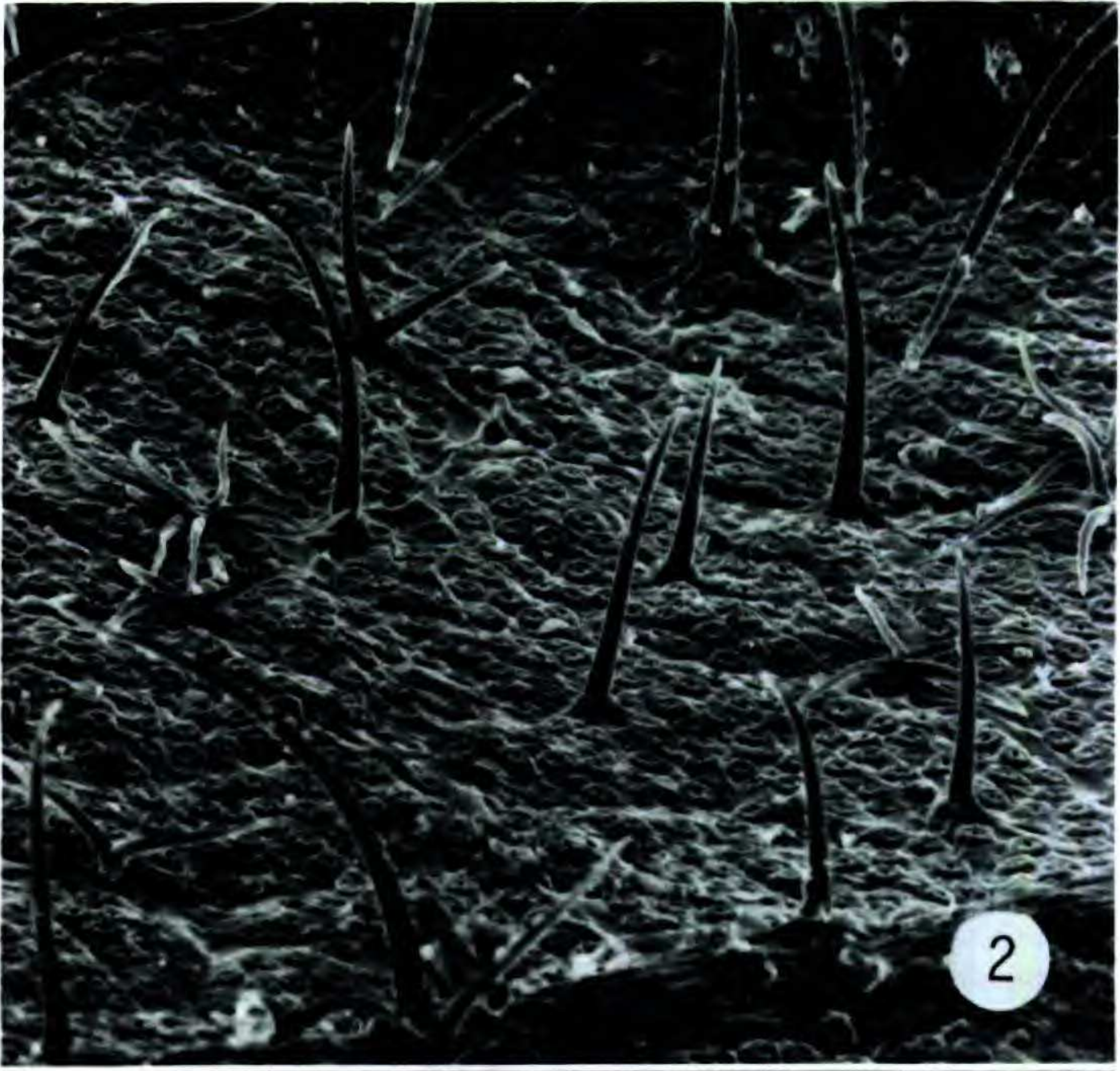
Type 12 (curly thin-walled unicellular). Trichomes of this type are thin-walled and collapse upon drying even in mature leaves. There is no evidence of glandular function. These persistent trichomes are coiled and unicellular. They occur in abundance only on type IV *Nothofagus* leaves, where they form dense mats over the lower surface (Figs. 30–32).

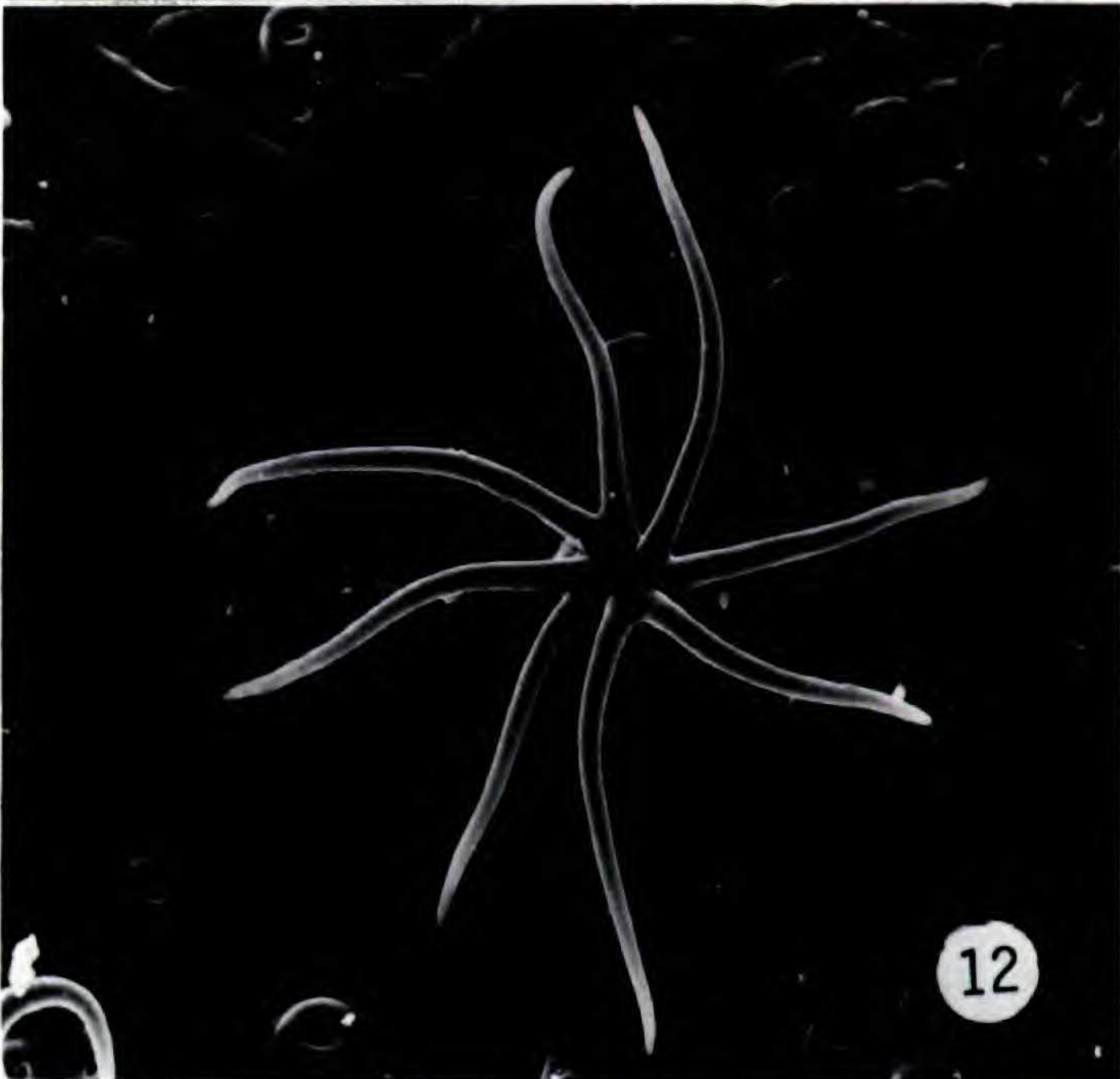
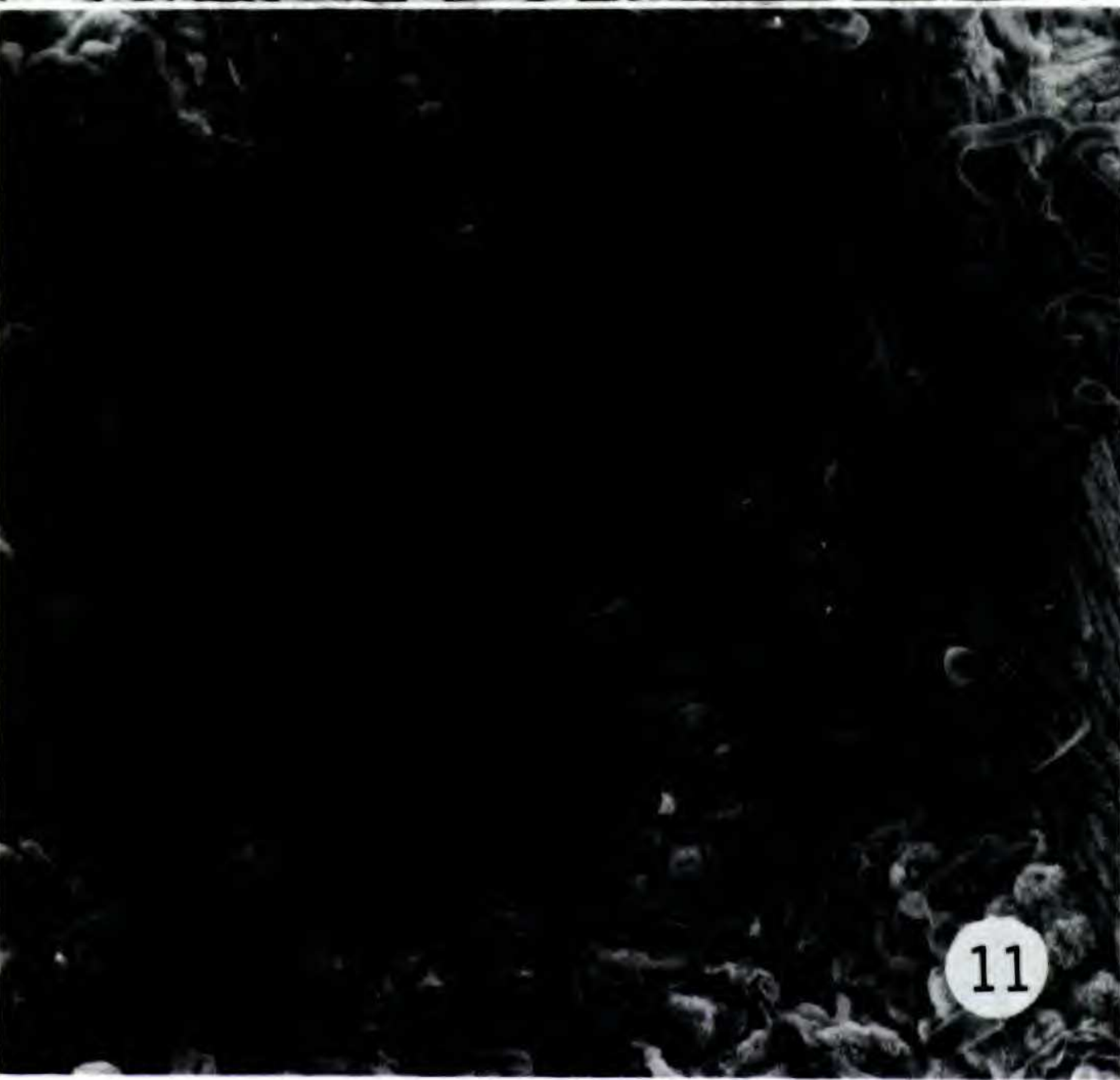
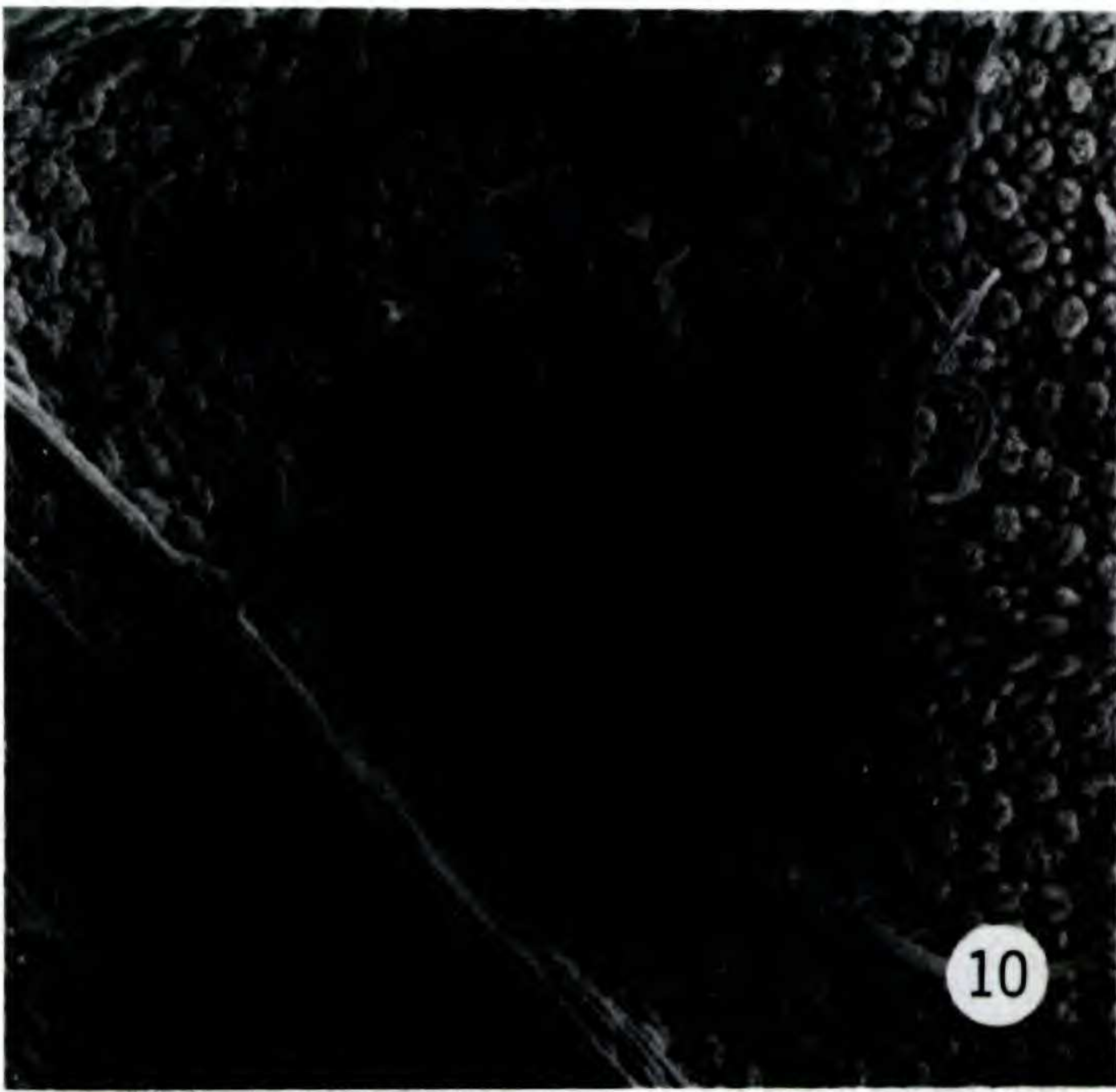
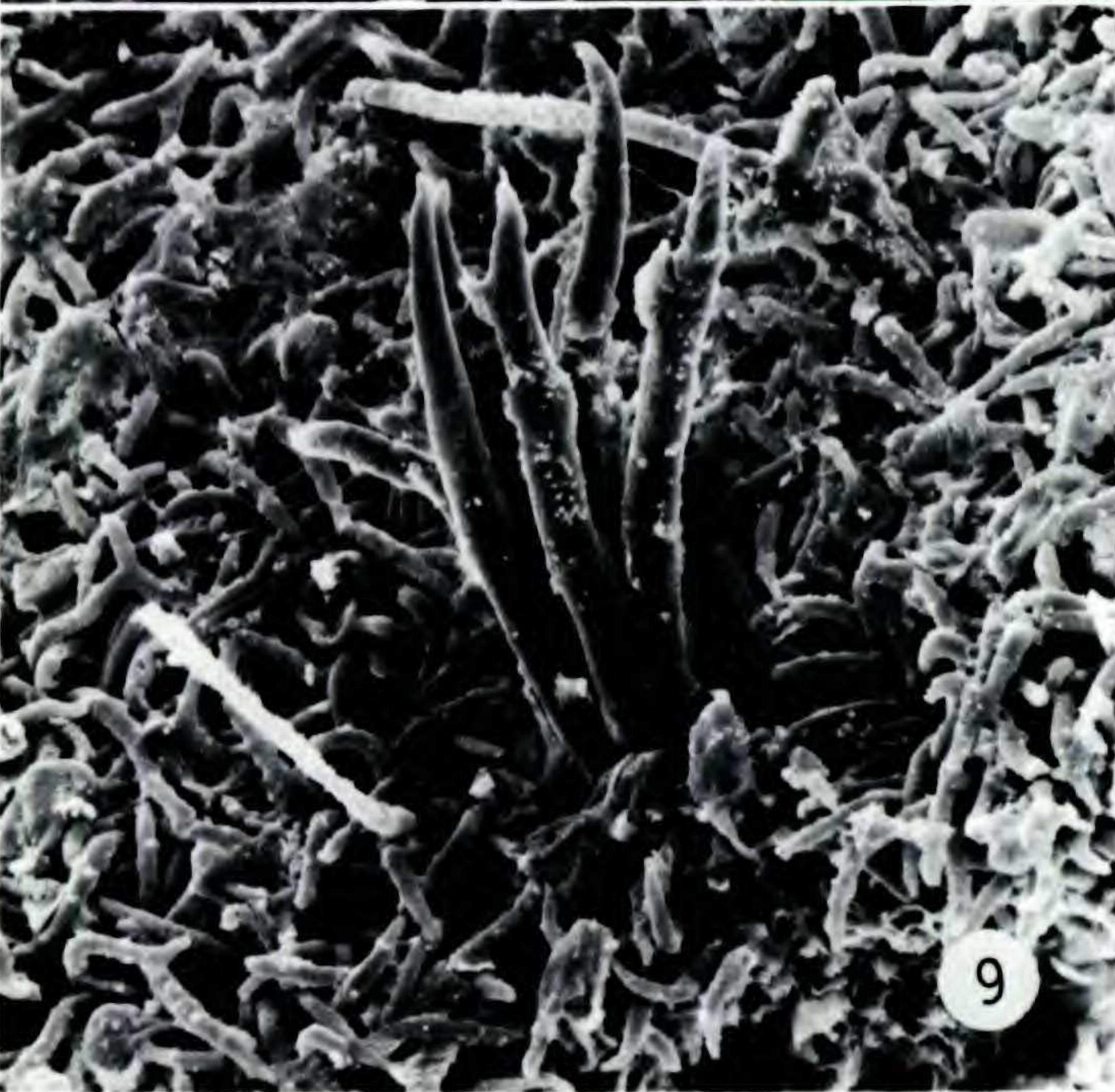
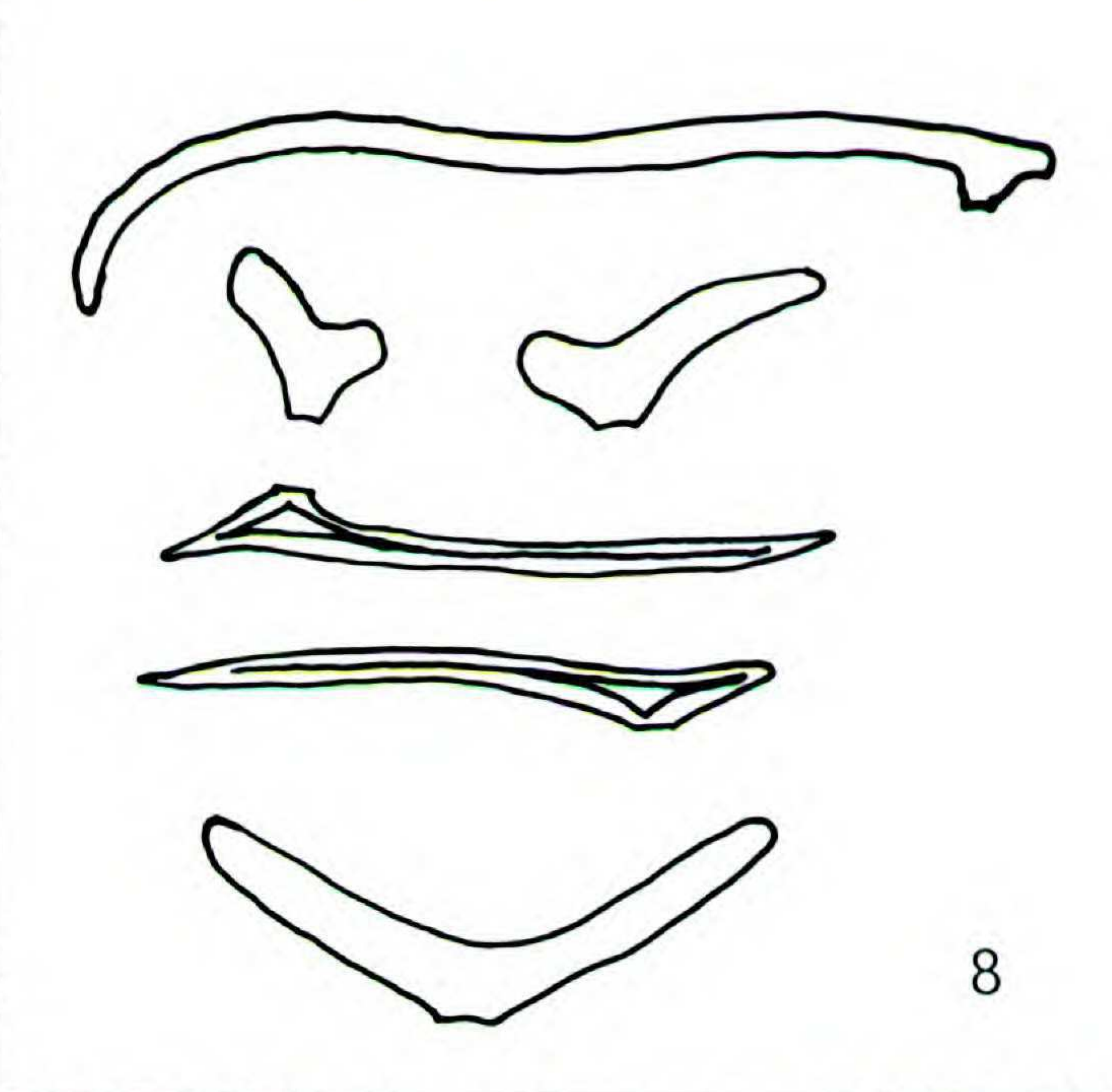
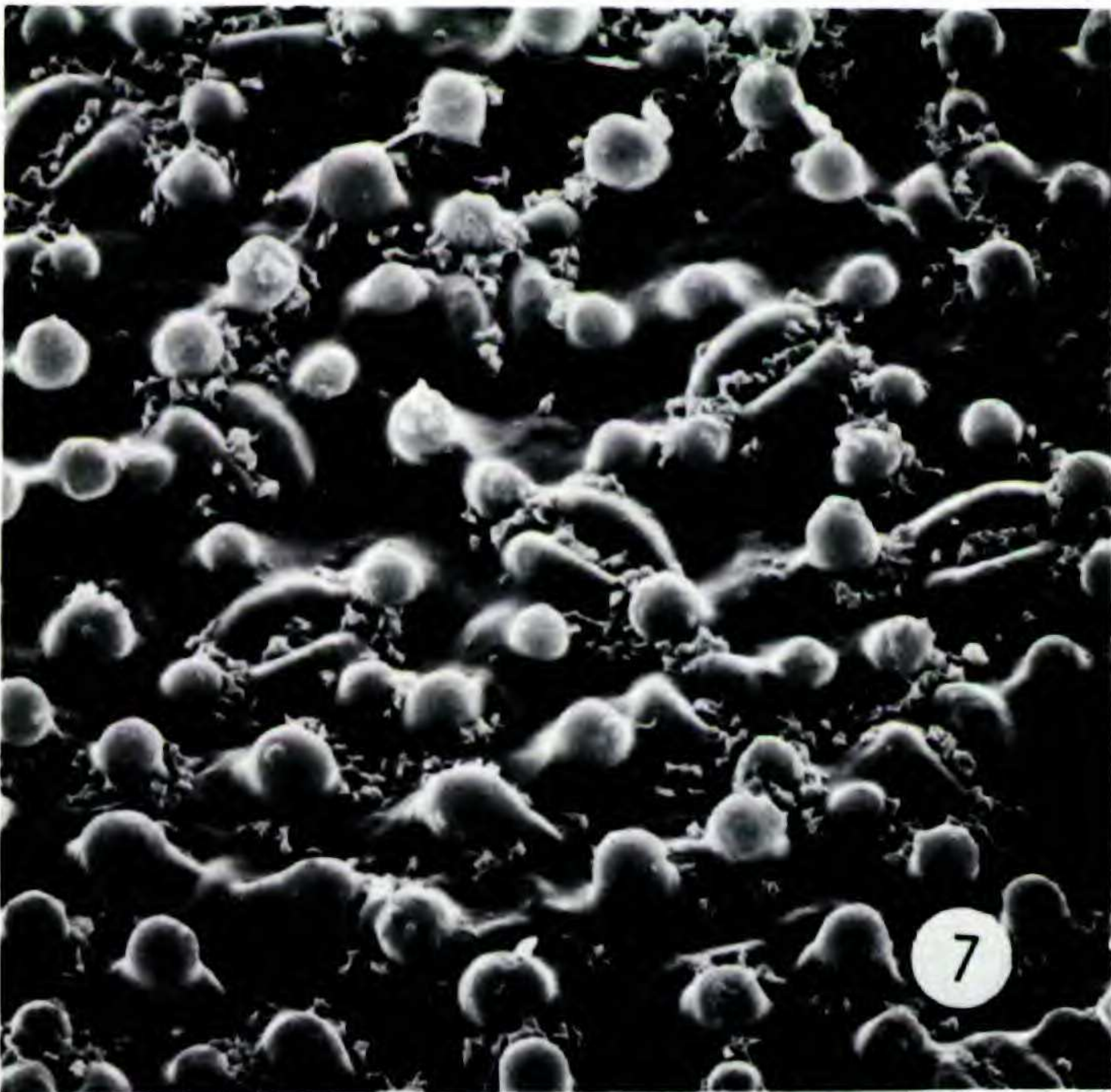
Type 13 ("thin"-walled peltate). This trichome type

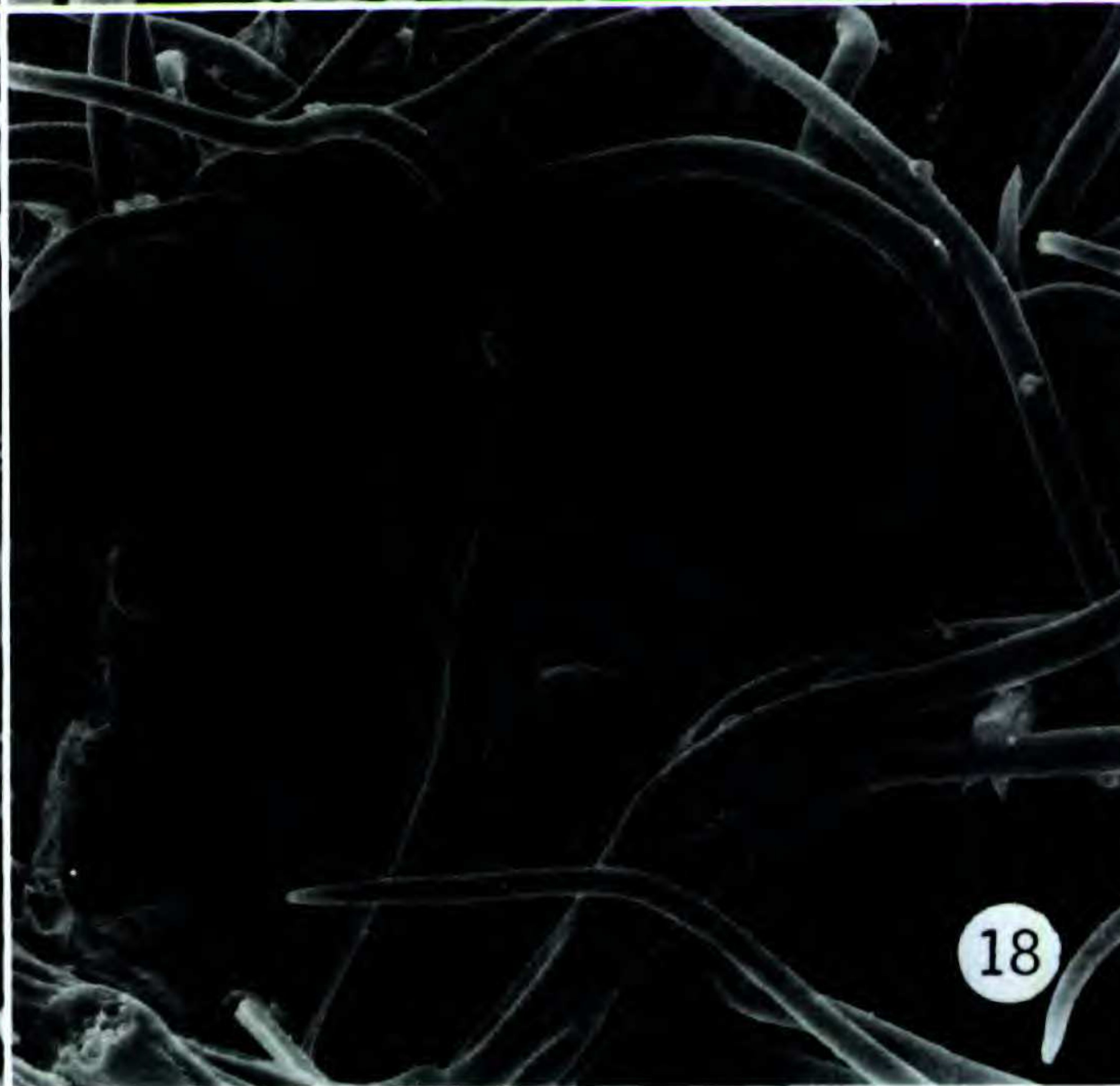
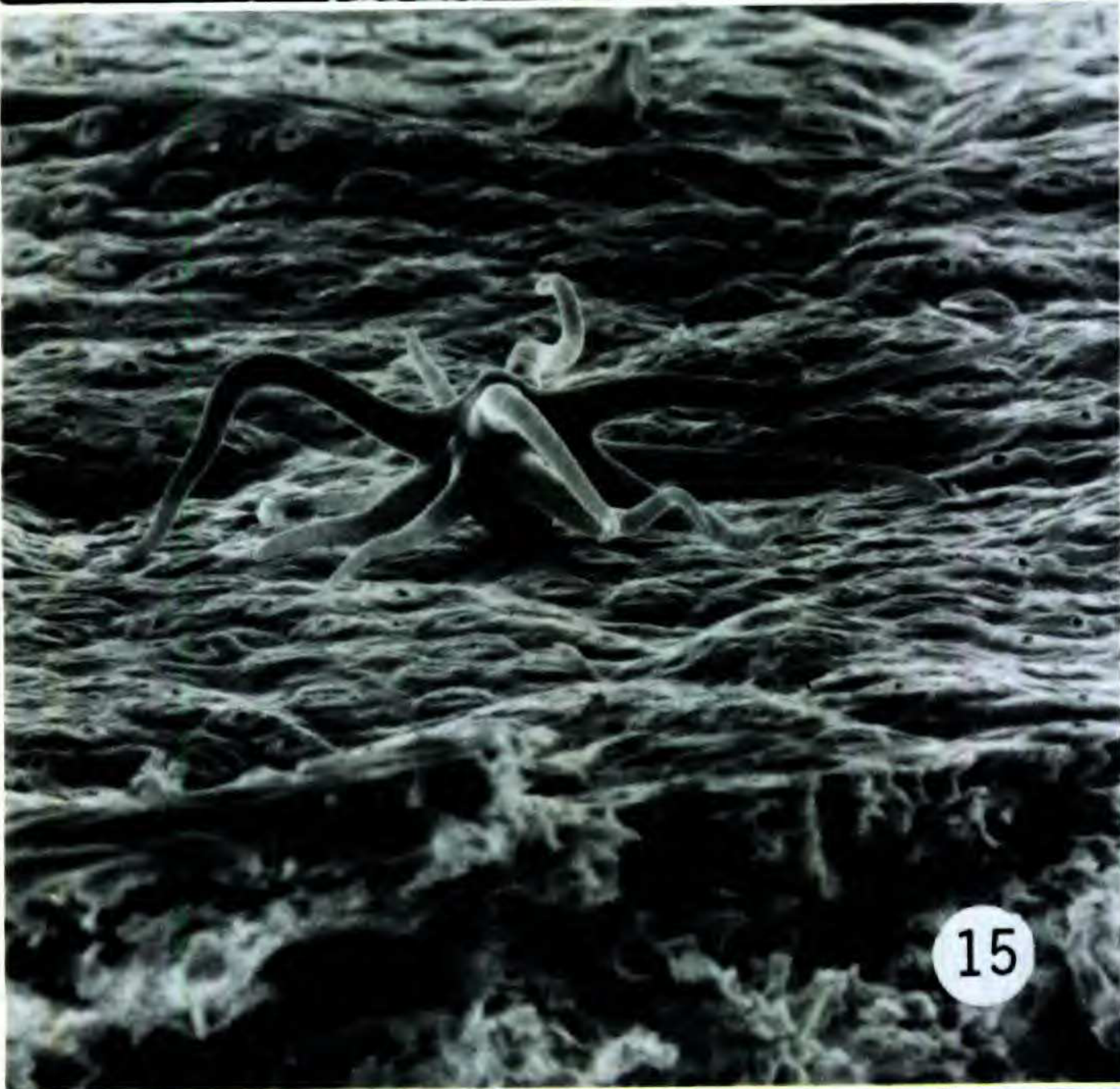
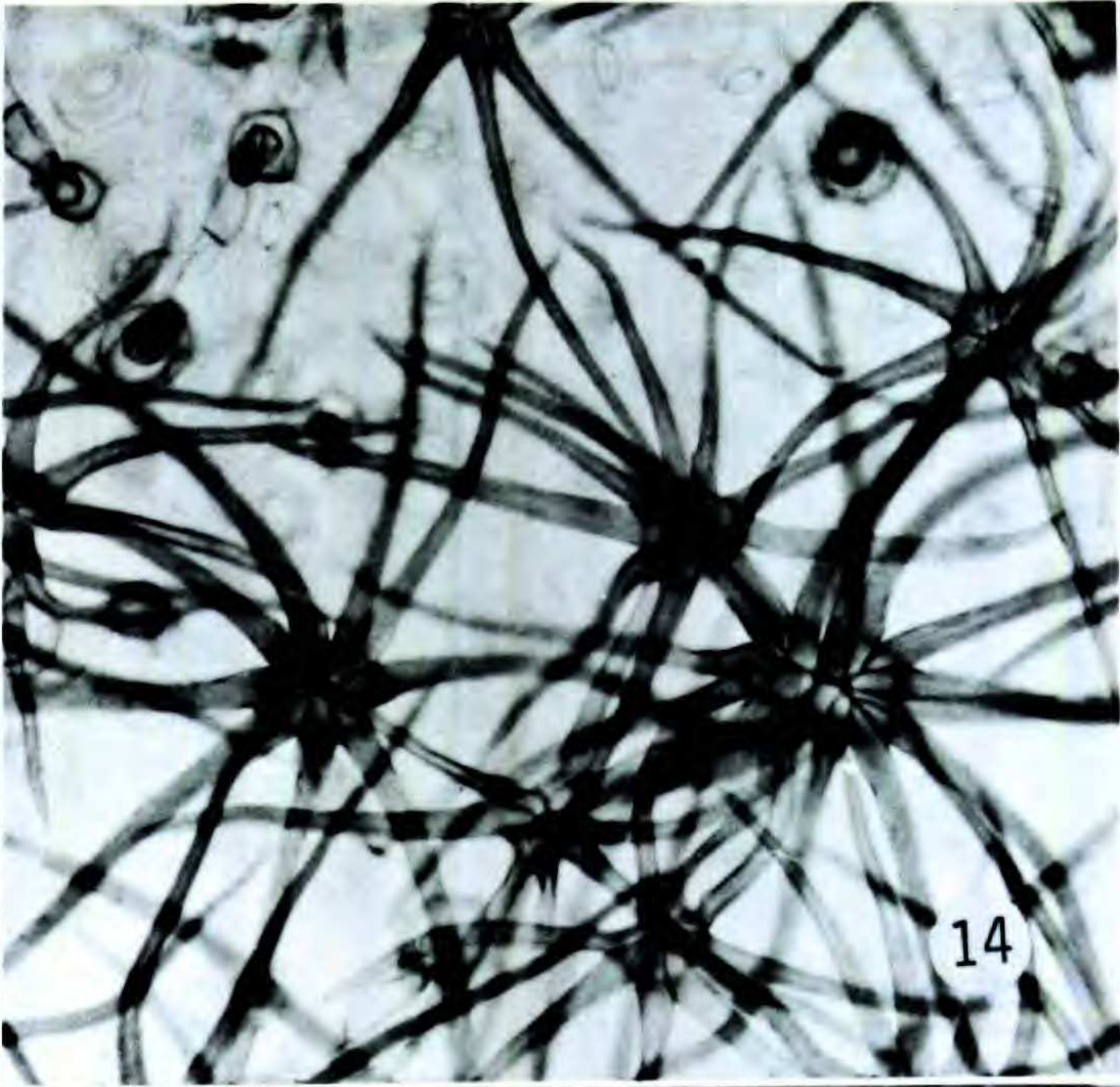
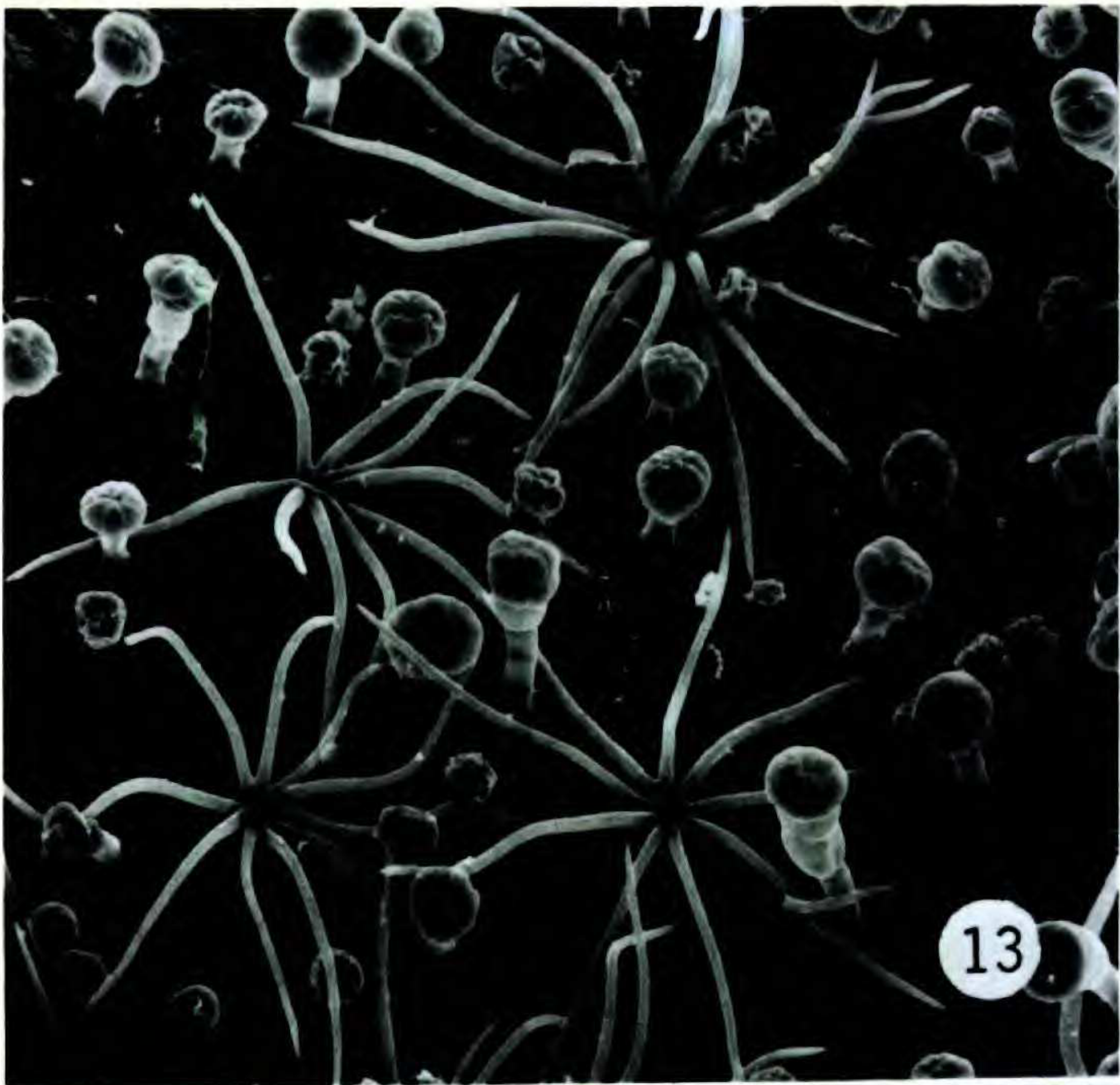
FIGURES 1–6.—1. Photomicrograph of solitary unicellular (type 1) trichomes over a secondary vein in *Nothofagus alessandri* (3115); note also the large globular (type 17) trichomes over the fine venation, 250 $\times$.—2. Scanning electron micrograph of short erect type 1 trichomes over fine venation, *Castanea mollissima* (110), 125 $\times$.—3. Photomicrograph of type 1 trichomes on the margin of *Nothofagus alessandri* (3115), 100 $\times$.—4. Scanning electron micrograph of unicellular conical (type 2) trichomes on *Nothofagus pumilio* leaves (3131), 500 $\times$.—5. Photomicrograph of type 2 trichomes showing broad basal portions, upper cuticle of *Nothofagus antarctica* (3117), 250 $\times$.—6. Photomicrograph of papillae (type 3 "trichomes") on the lower epidermis of *Quercus myrsinaefolia* (1183), 640 $\times$. [Note: Numbers in parentheses are Indiana University Paleobotanical Extant Leaf Collection accession numbers. See Jones (1984) for herbarium and collector information.]

FIGURES 7–12.—7. Scanning electron micrograph of papillae on the lower surface of *Quercus myrsinaefolia* (1183), 500 $\times$.—8. Appressed laterally attached unicellular (type 4) trichomes (redrawn from Camus, 1934), ca. 200 $\times$.—9. Scanning electron micrograph of a "closed" fasciculate (type 5) trichome from the lower surface of *Lithocarpus sundaicus* (3110), 250 $\times$.—10. Scanning electron micrograph of an "open" fasciculate trichome from the lower surface of *Quercus alba* (137), 125 $\times$.—11. Scanning electron micrograph of a type 5 trichome with long intertwining elements, *Quercus benthami* (631), lower surface, 125 $\times$.—12. Scanning electron micrograph of a stellate (type 6) trichome from *Castanea mollissima* (110), lower surface, 250 $\times$.

FIGURES 13–18.—13. Scanning electron micrograph of sprawling type 6 trichomes interspersed among type 16 trichomes, upper leaf surface of *Castanea mollissima* (110), 250 $\times$.—14. Photomicrograph of type 6 trichomes showing prominent pie-shaped wedges at the juncture of the elements, lower cuticle of *Castanea ozarkensis* (111), 250 $\times$.—15. Scanning electron micrograph of a bilayered stellate (type 6) trichome on the lower leaf surface of *Quercus arkansana* (610), 250 $\times$.—16. Scanning electron micrograph of a fused stellate (type 7) trichome on the lower foliar surface of *Quercus fusiformis* (3144), 500 $\times$.—17. Photomicrograph of type 7 trichomes on the lower leaf surface of *Quercus fusiformis* (3144), 250 $\times$.—18. Scanning electron micrograph of stipitate fasciculate (type 8) trichomes on the lower leaf surface of *Quercus crassipes* (640), 250 $\times$.







consists of thin-walled cells. They possess uniseriate stalks and irregularly shaped stellate to discoidal caps composed of many randomly oriented cells (Fig. 33). This type is easily distinguished from type 11 trichomes by the lack of thick cell walls and regular, radially-fused cap cells. They are relatively large and collapse upon drying to form, collectively, a rough mat (Fig. 34). They are extremely difficult to isolate and nearly impossible to distinguish individually by examining whole leaf material. They cover the lower surface of many *Castanopsis* and some *Lithocarpus* species. They are not found outside of the Castaneoideae although some type 19 trichomes (Fig. 53) of *Trigonobalanus* approach this type. When lost they leave round simple bases that give *Castanopsis* cuticles their characteristic speckled appearance (Fig. 35). Camus first (1928–1929) classified these as a “poils tecteurs” but later (1934–1954) discussed them under “poils secreteurs.” She called them “poils écailleux ou en ecusson” in the earlier work and “poils en bouclier a pedicelle court” in the latter.

Type 14 (rosulate). These trichomes consist of unicellular, often thin-walled elements, arranged in small bushy tufts (Figs. 36, 37). They are frequently dark in color and have a glistening appearance suggesting glandular function. They intergrade with tufts of types 5 and 10. They generally occur evenly dispersed over the lower surface of the leaf but are occasionally found on the upper surface as well. They are most abundant in the genus *Quercus* but also occur in some species of *Lithocarpus*.

C. “Glandular” trichomes. Trichomes of this group are generally multicellular, apparently glandular in function, and composed of thin-walled cells. Ca-

mus (1928–1929, 1934–1954) used the term “poils secreteurs” for trichomes of this type. She did not, for the most part, distinguish the various forms that fall into this category. As Hardin (1976) indicated, this is probably because they intergrade so thoroughly.

Type 15 (simple uniseriate). These trichomes consist of a single column of two or more (generally four or five) thin-walled, apparently glandular cells of nearly equivalent size (Figs. 38, 39). This trichome type intergrades with type 16, which possesses an enlarged terminal cell (or group of cells) or alternatively contains a multiseriate section. The form of type 15 trichomes varies considerably. They may be short and consist of nearly spherical cells, to long and composed of elongate cylindrical cells (Figs. 40, 41). The terminal cells of some forms taper to a point whereas others are rounded and slightly enlarged. When lost, particularly in the preparation of isolated cuticles, they often leave behind a resistant cutinized basal portion (Fig. 42). They are usually distributed evenly over the fine venation on the lower foliar surface. They also are found on the upper surface in many species, but when present they generally occur in much fewer numbers. This is the most basic of the “glandular” types and can be found in all three subfamilies. It reaches its greatest development in the Fagoideae and Quercoideae. Hardin’s (1976) type, of the same name, is equivalent.

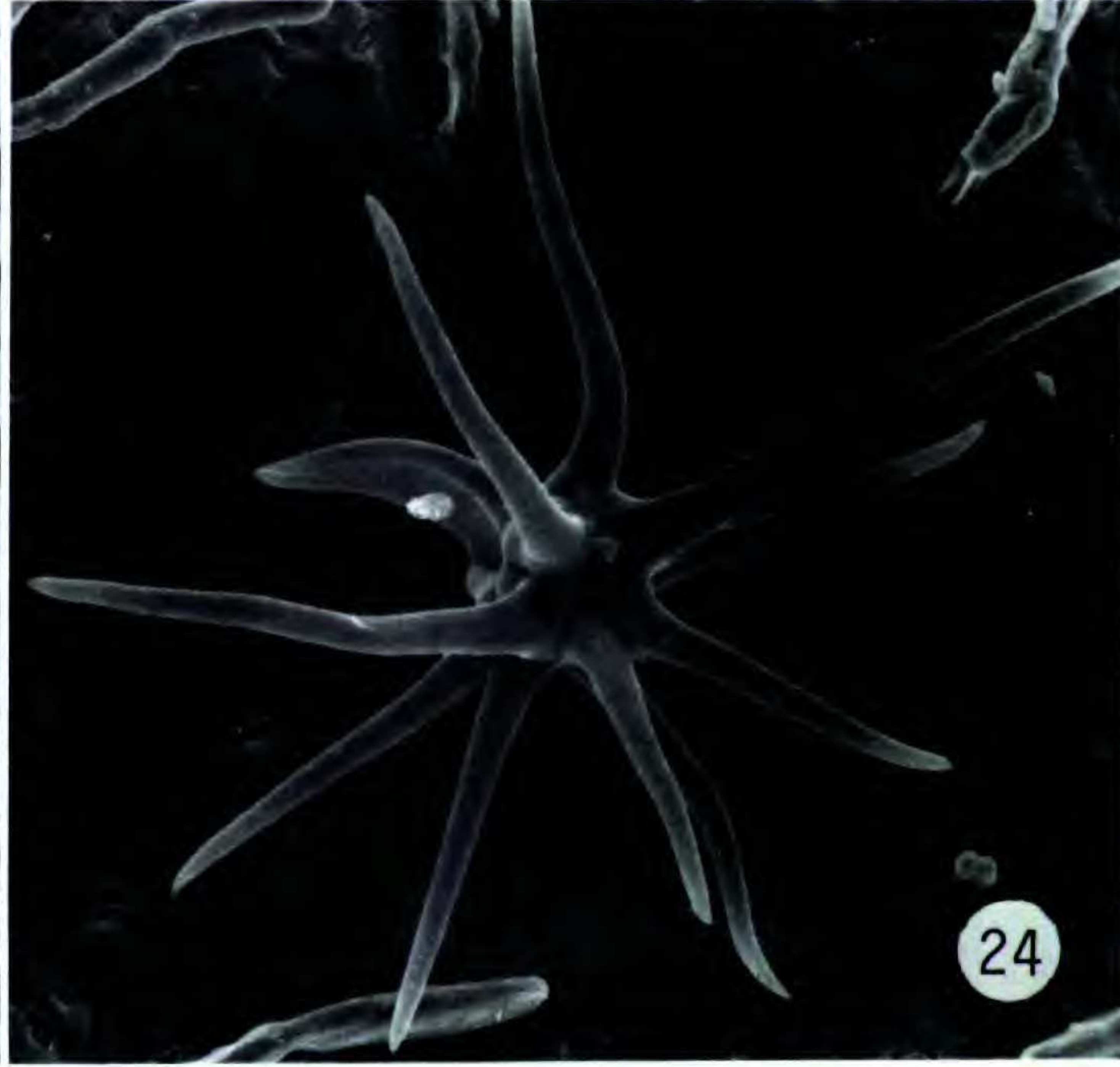
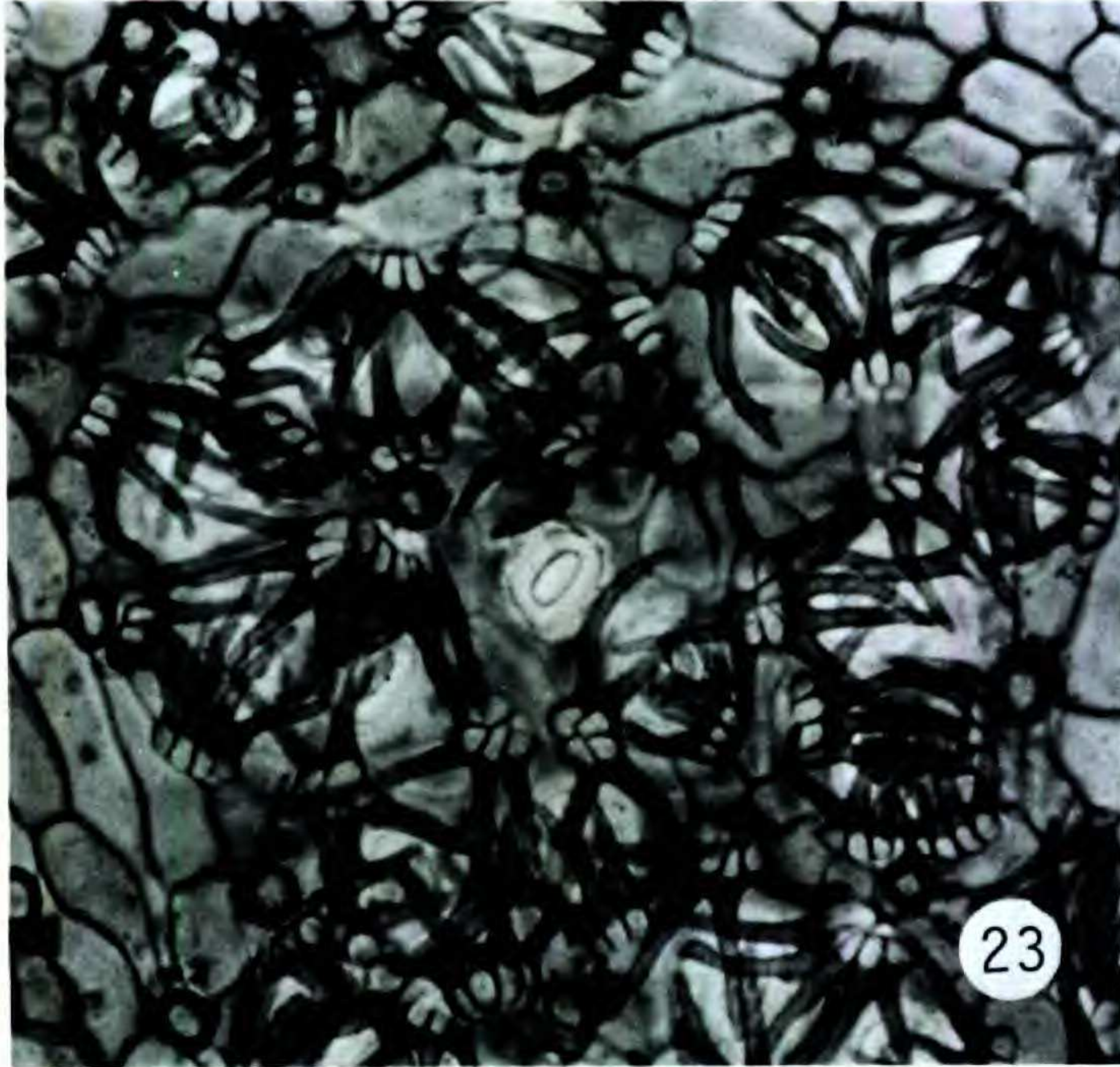
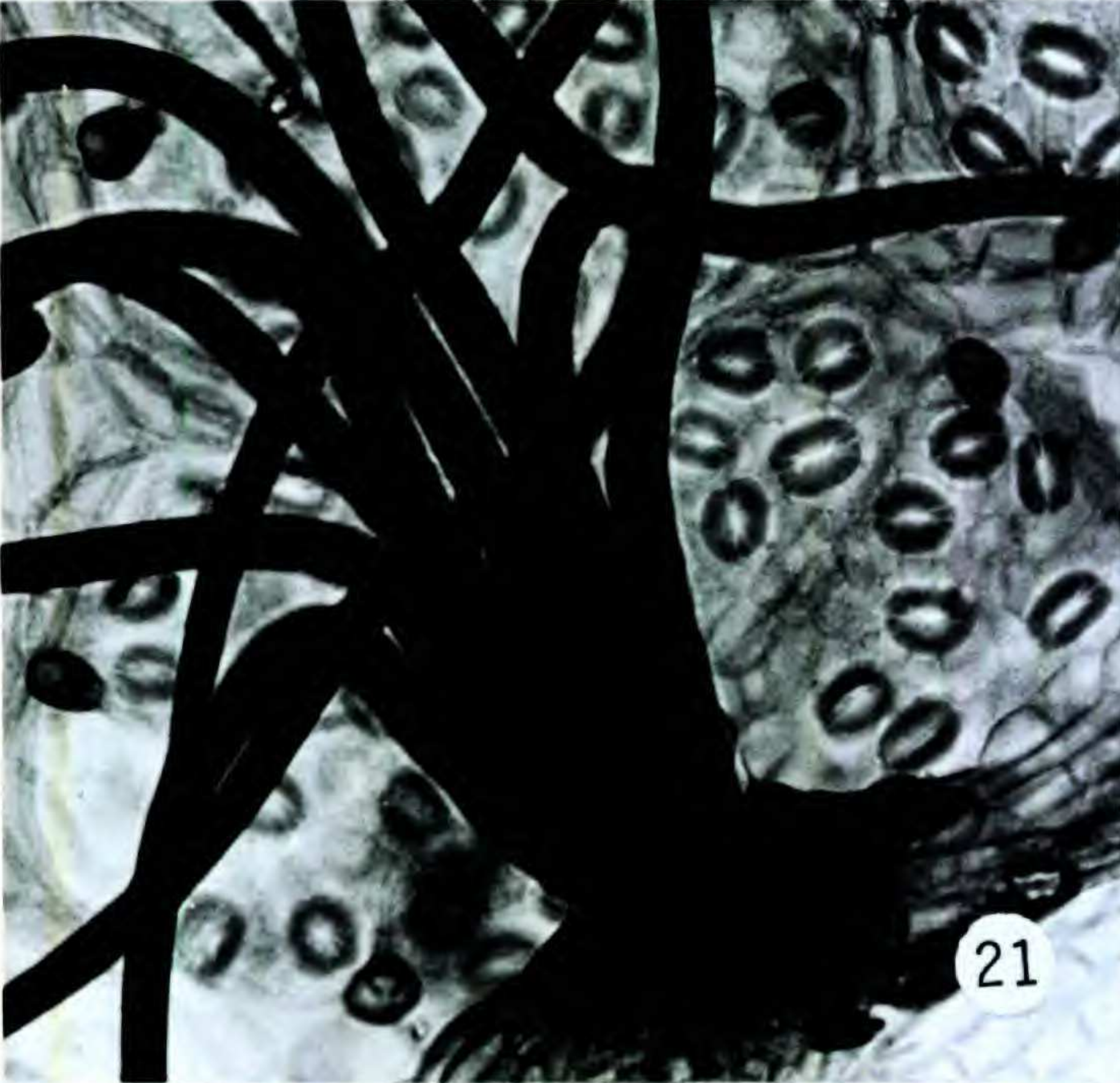
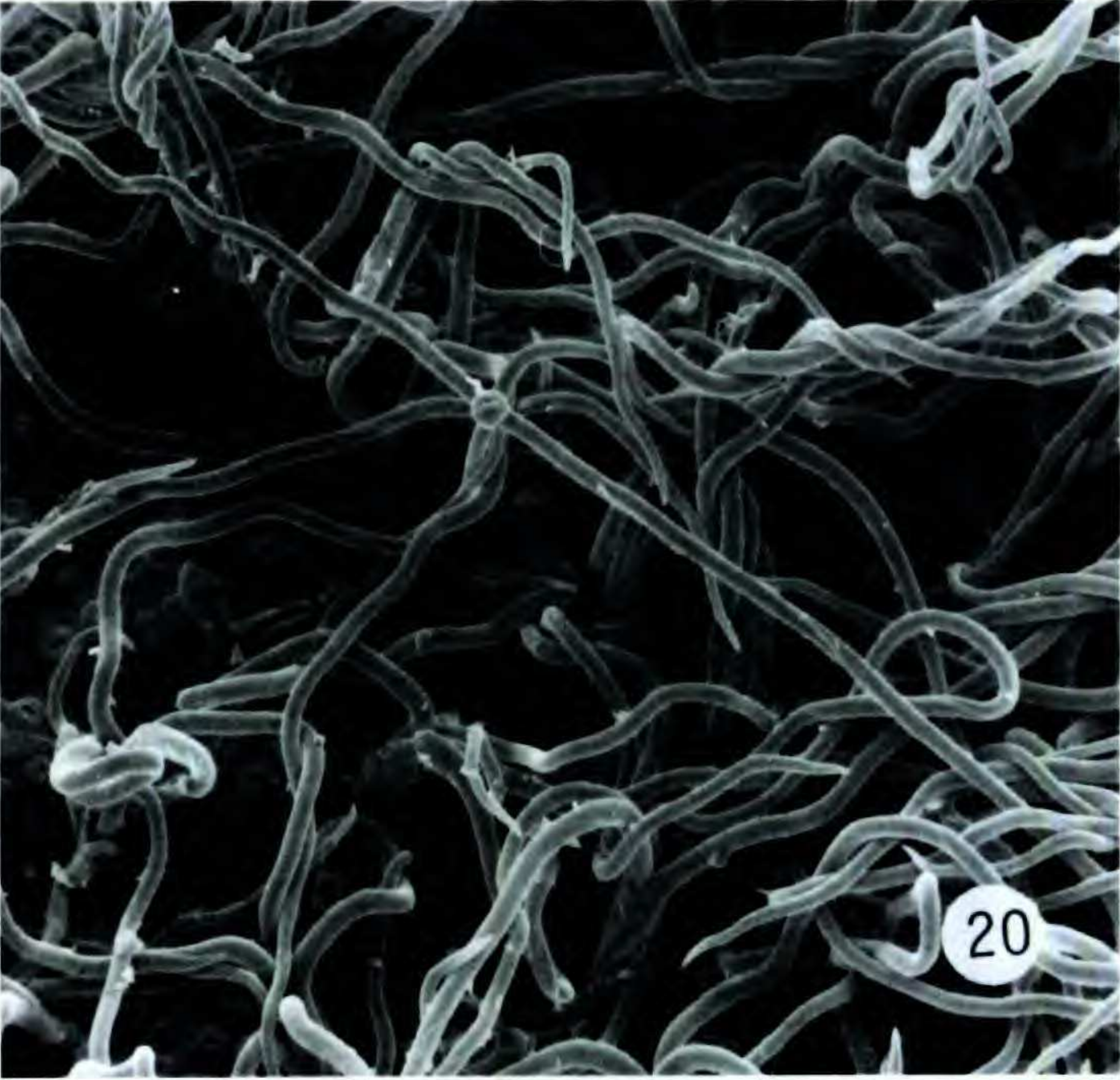
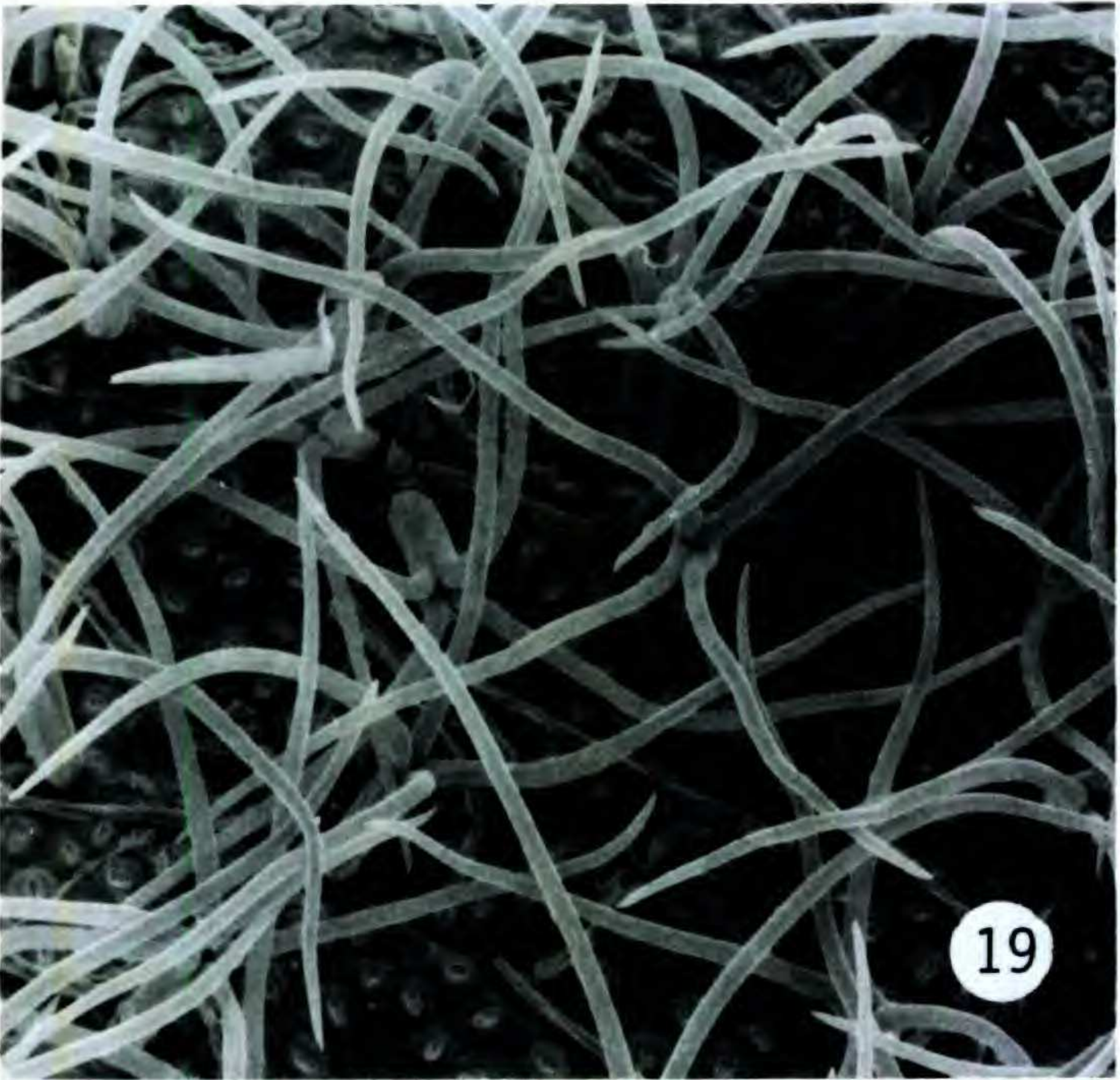
Type 16 (capitate or irregularly multiseriate). This type consists of a rather heterogeneous group of trichomes, the various forms of which are found together often and intergrade. As envisioned here, type 16 trichomes consist of uniseriate stalks with a single markedly enlarged terminal cell, or a group of terminal cells,

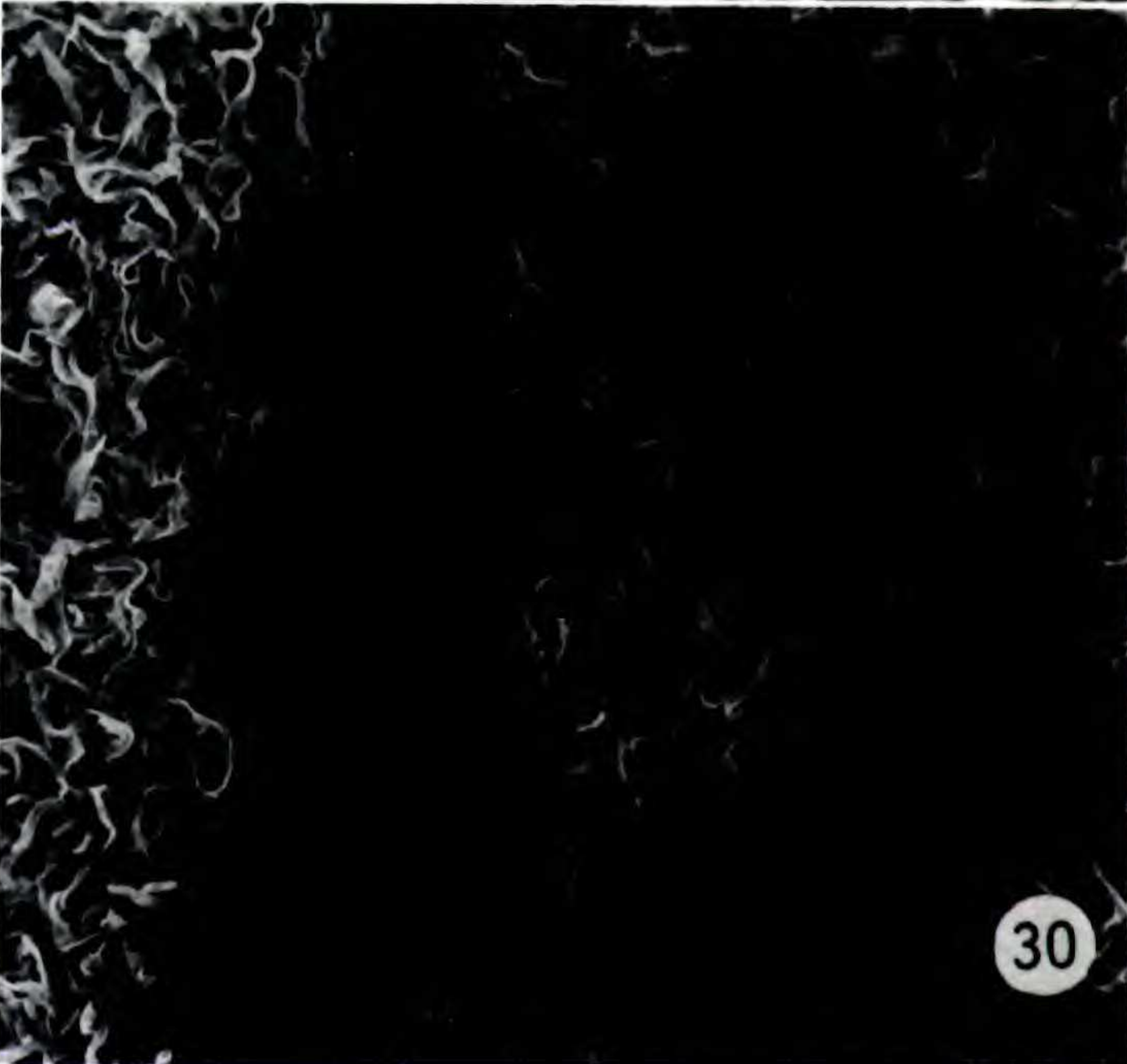
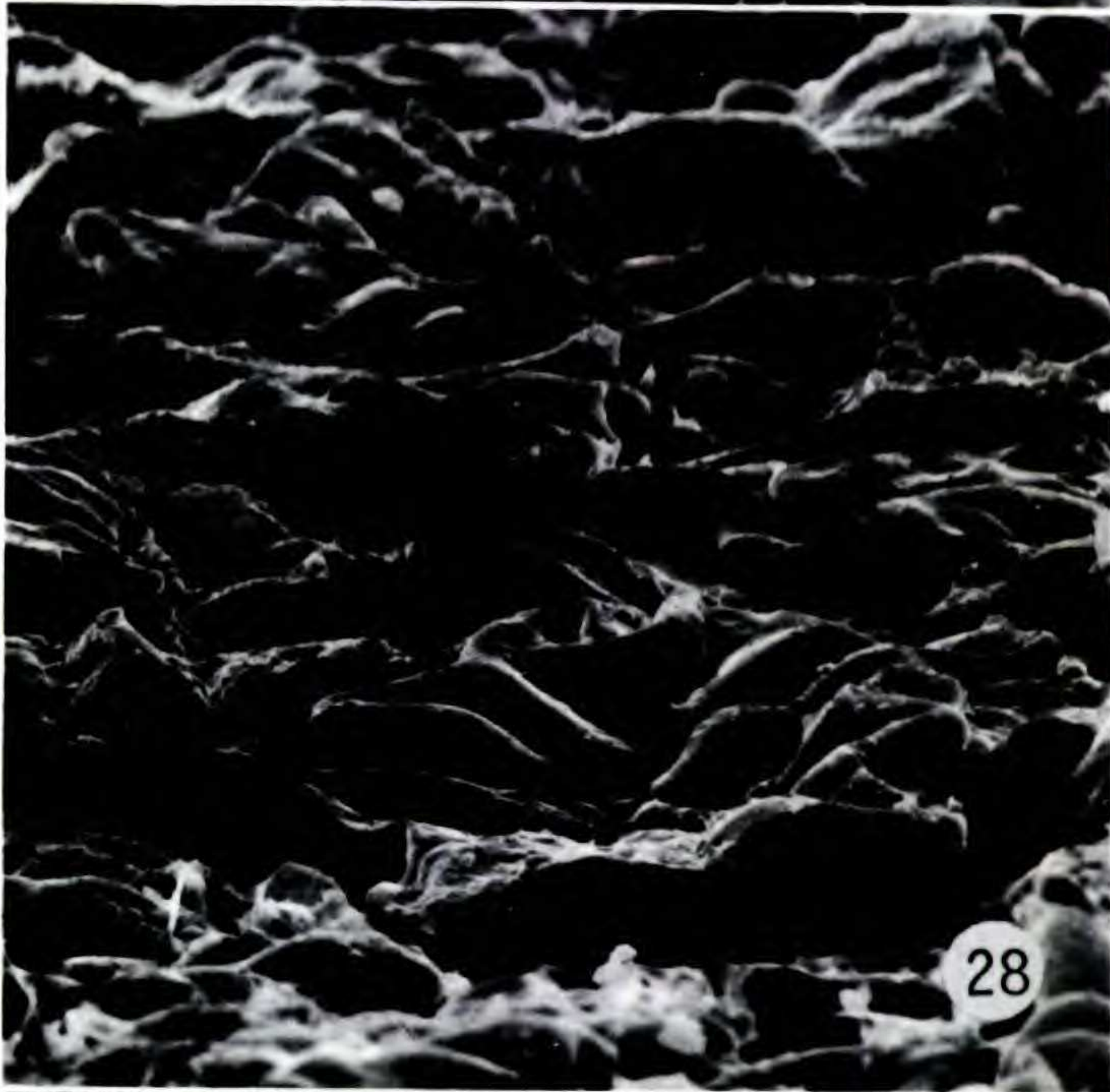
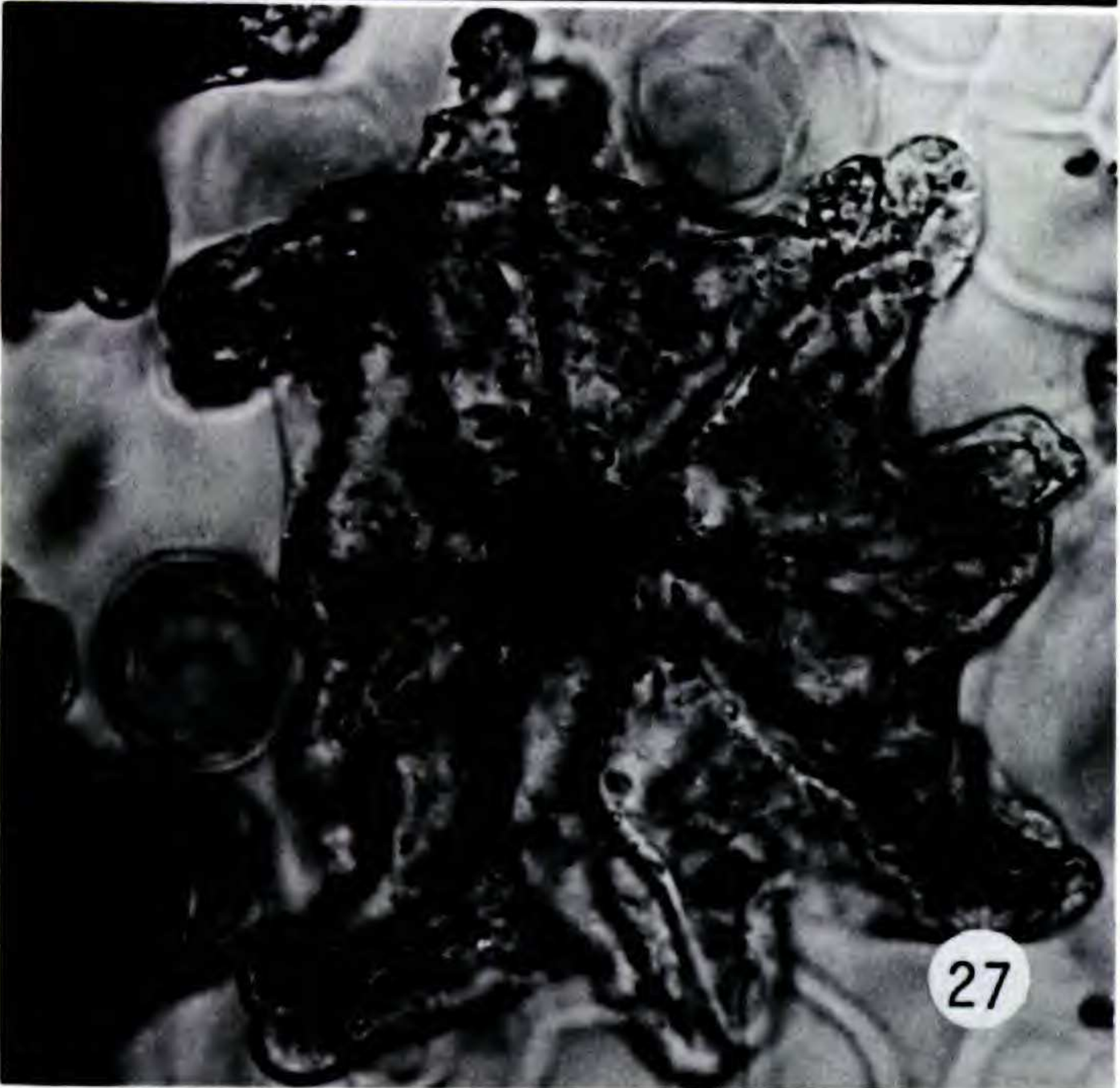
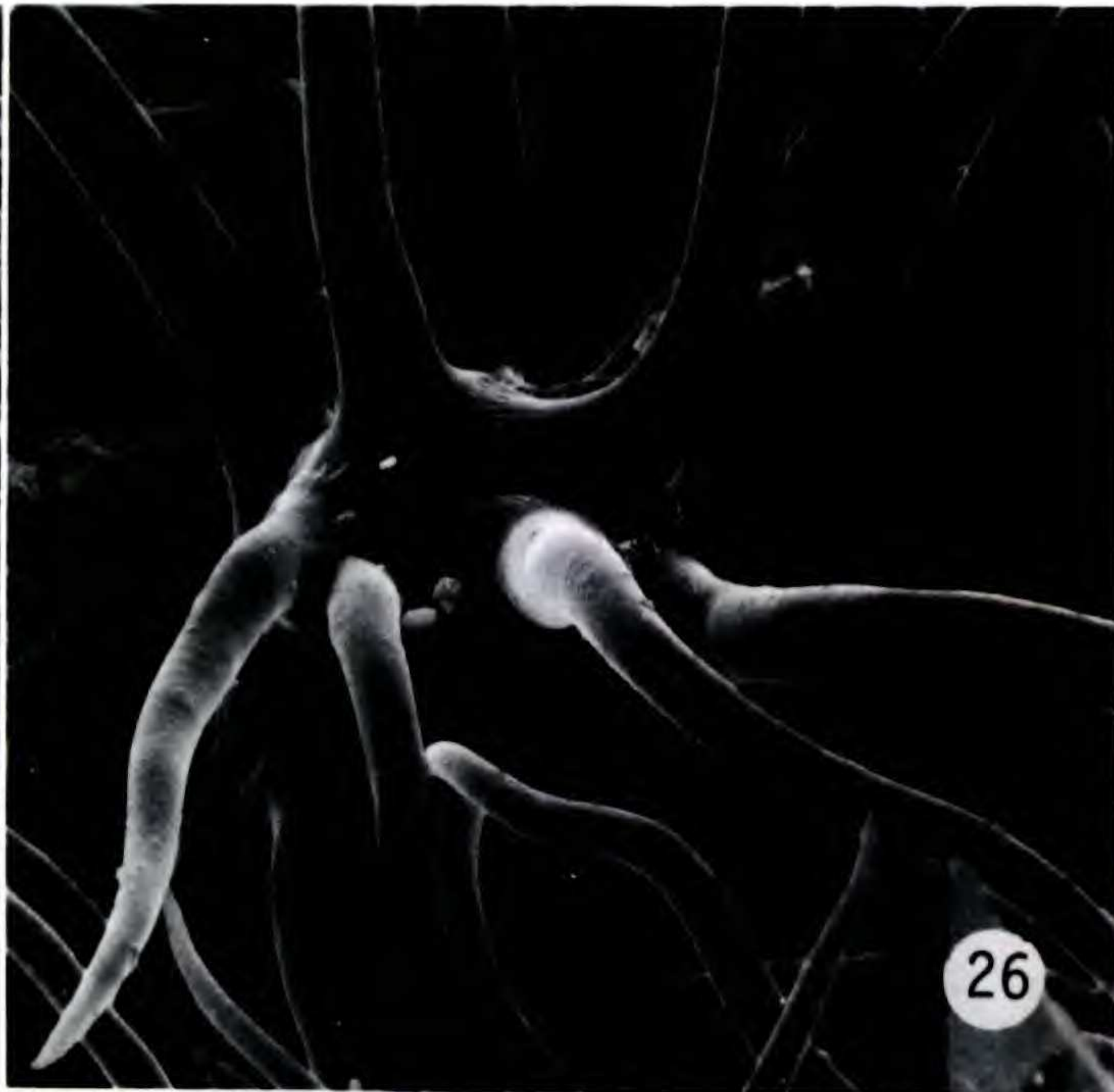
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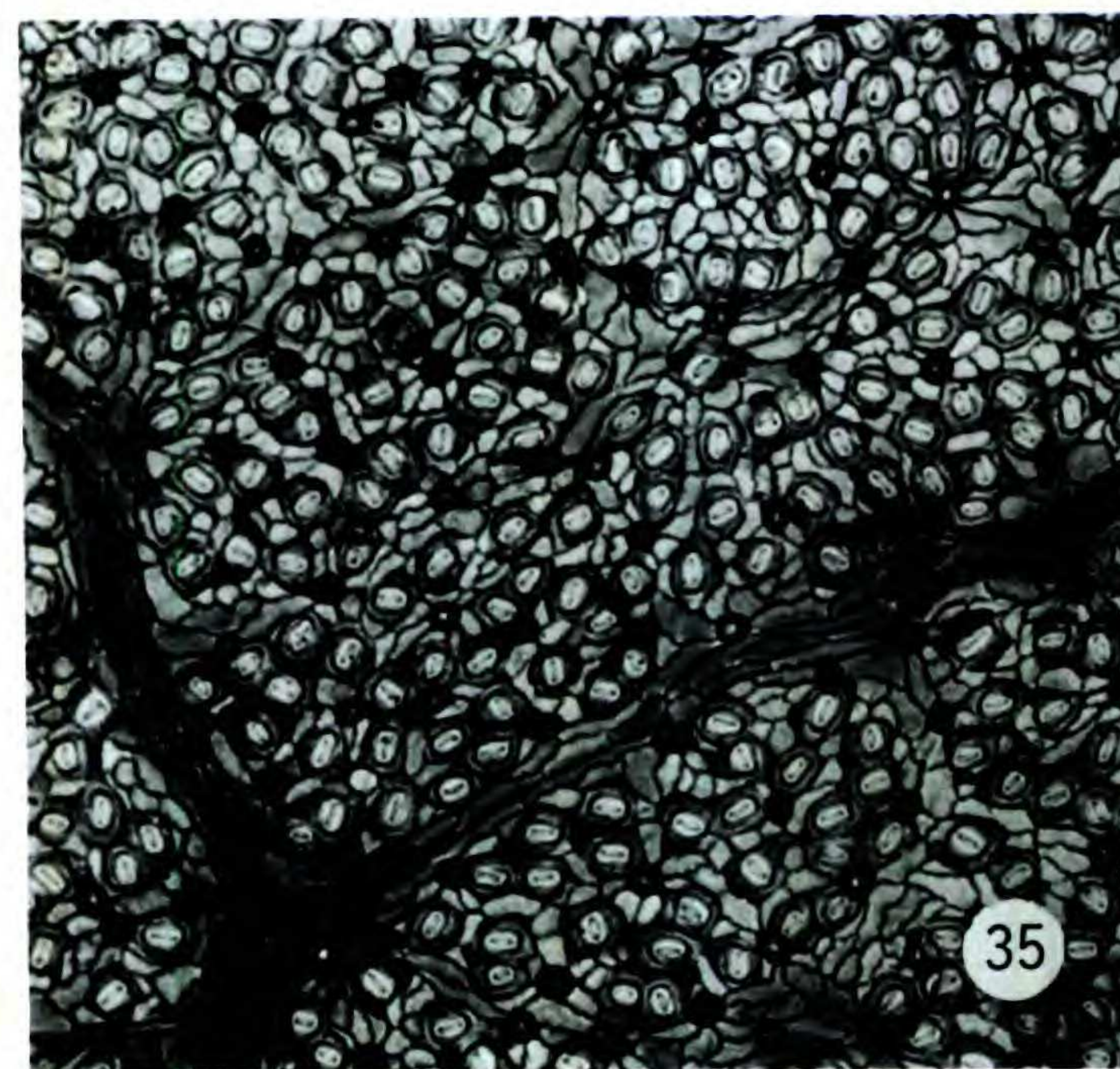
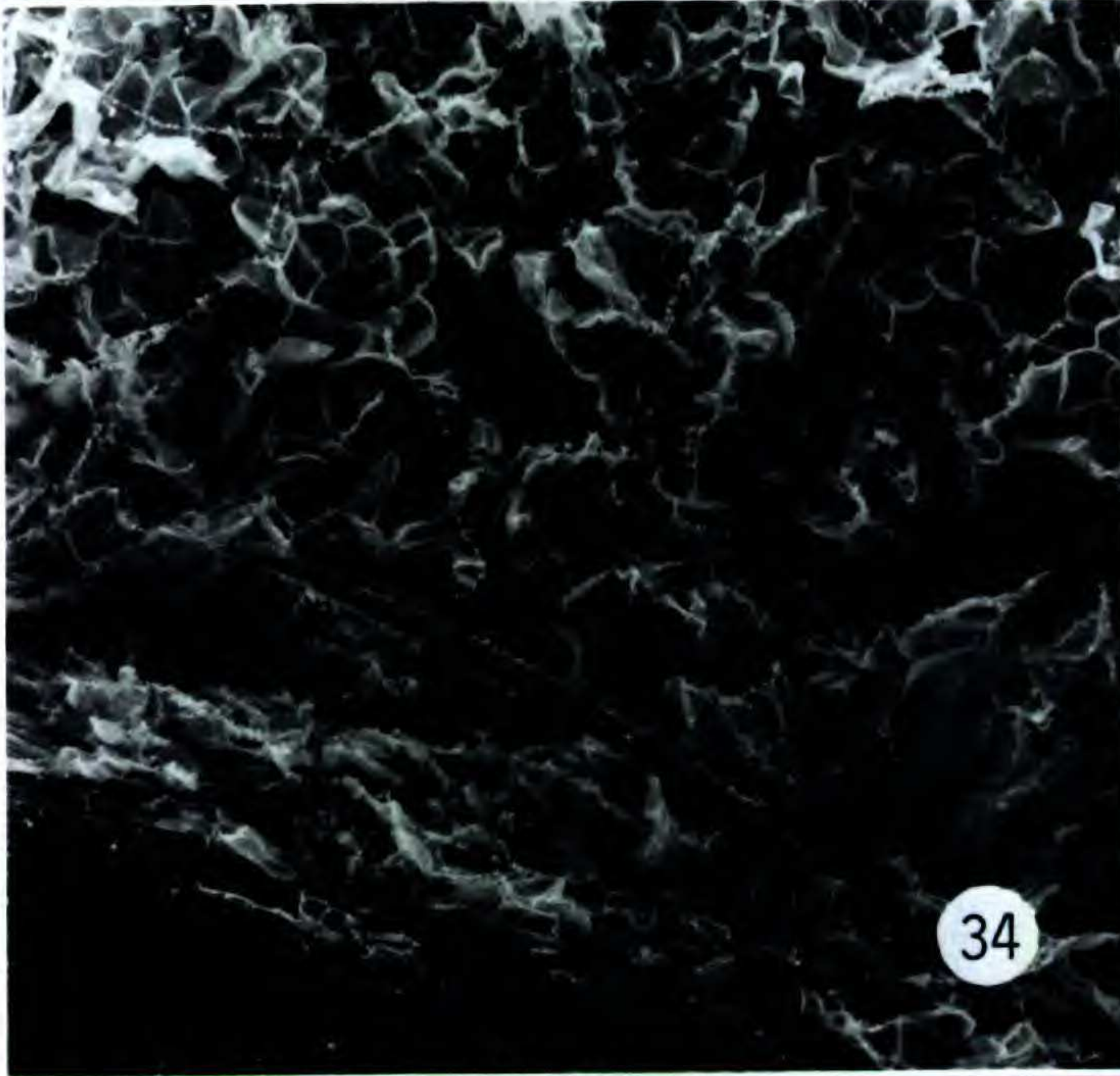
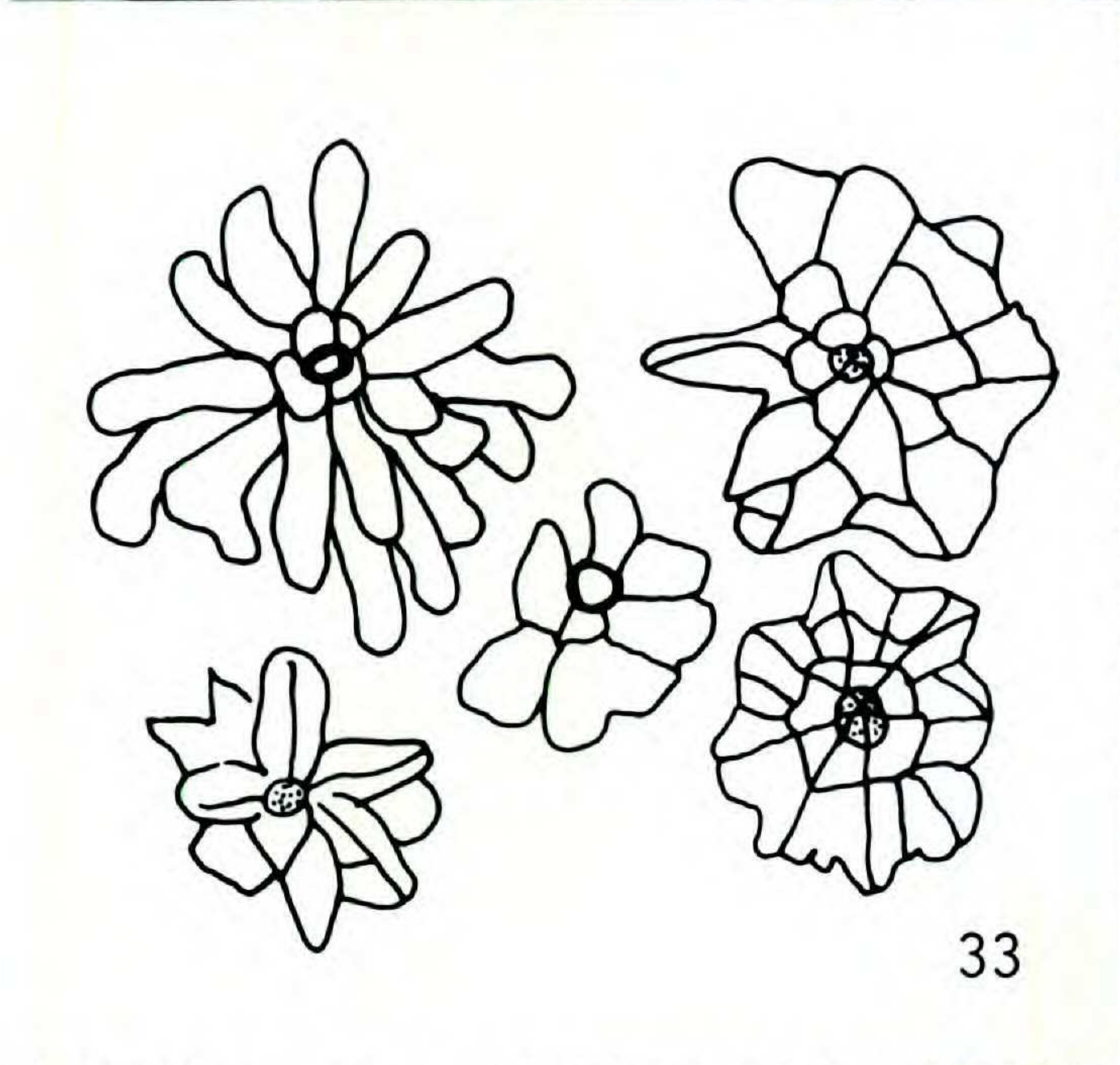
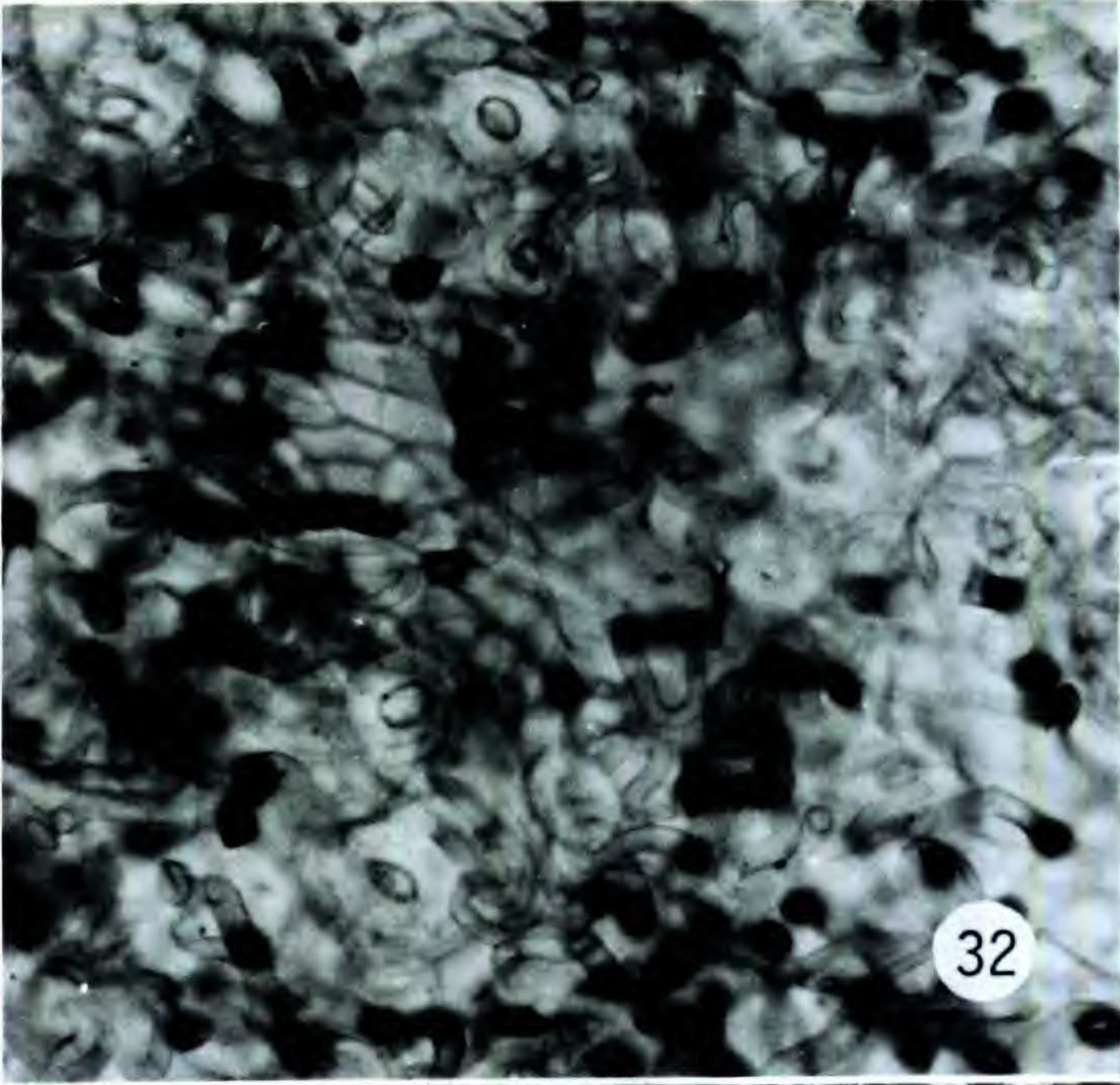
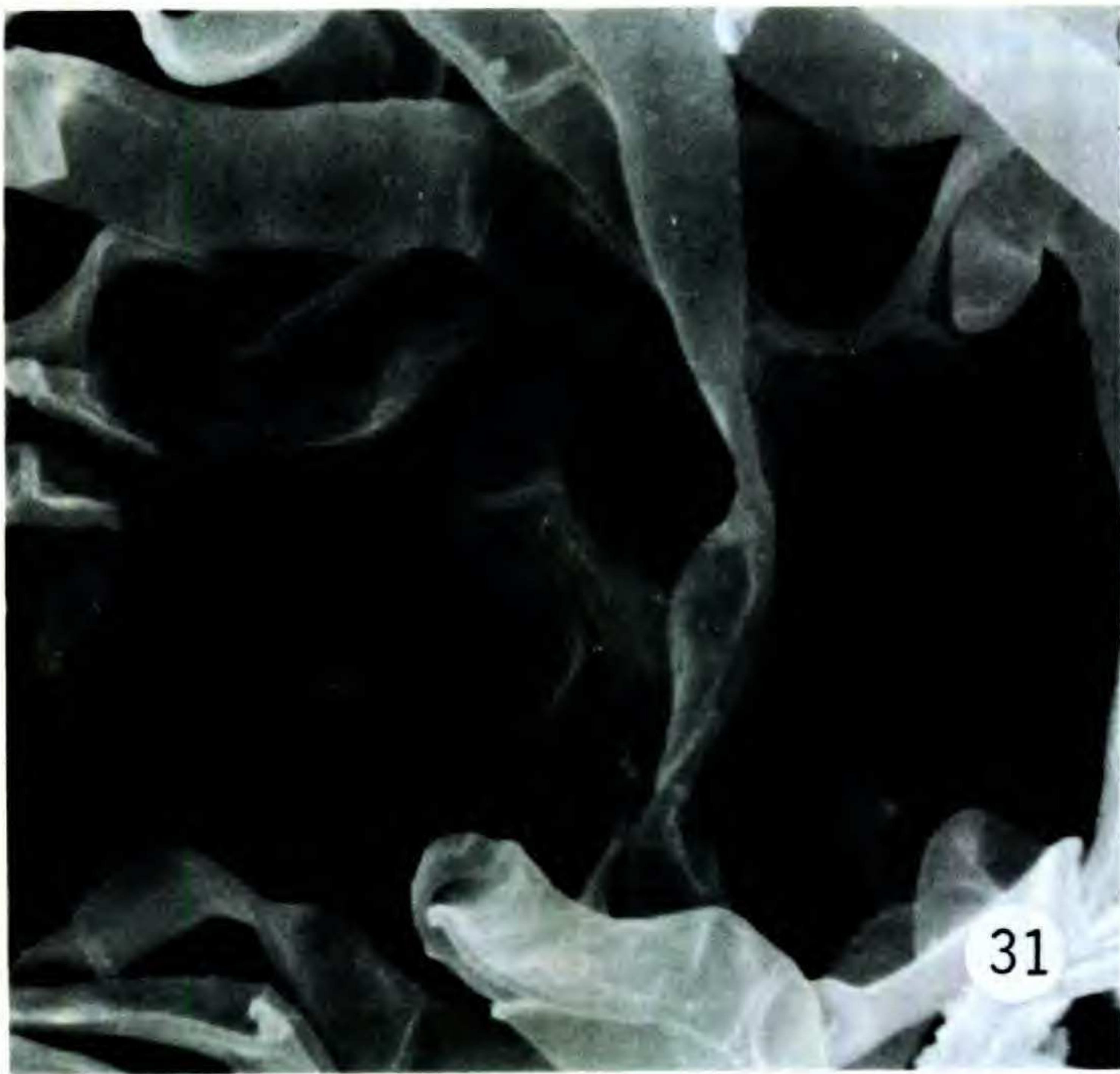
FIGURES 19–24.—19. Scanning electron micrograph of type 8 trichomes scattered over fine veins on the lower leaf surface of *Quercus imbricaria* (3148), 125 $\times$.—20. Scanning electron micrograph of type 8 trichomes with long intertwining elements, *Quercus craspopilus* (644), 125 $\times$.—21. Photomicrograph of a type 8 trichome with a pedicellate base, lower foliar surface of *Quercus margaretta* (2324), 250 $\times$.—22. Scanning electron micrograph of appressed parallel tufts (type 9 trichomes) on the lower leaf surface of *Lithocarpus henryi* (1169), 1,000 $\times$.—23. Photomicrograph of type 9 trichomes showing the linear arrangement of elements, lower surface of *Lithocarpus encleisocarpus* (3095), 250 $\times$.—24. Scanning electron micrograph of a multiradiate (type 10) trichome on the lower leaf surface of *Quercus emoryi* (617), 250 $\times$.

FIGURES 25–30.—25. Scanning electron micrograph of large multiradiate (type 10) trichomes found on the lower leaf surface of *Lithocarpus densiflorus* (492), 125 $\times$.—26. Scanning electron micrograph of the rounded base of a large multiradiate trichome from the lower leaf surface of *Lithocarpus densiflorus* (492), 500 $\times$.—27. Photomicrograph of a “thick” walled peltate (type 11) trichome characteristic of the genus *Chrysolepis*, *C. sempervirens* (1207), 650 $\times$.—28. Scanning electron micrograph of type 11 trichomes on lower foliar surface of *Chrysolepis chrysophylla* (505), 500 $\times$.—29. Scanning electron micrograph showing a dense covering of type 11 trichomes on the lower foliar surface of *Chrysolepis chrysophylla* (505), 125 $\times$.—30. Scanning electron micrograph of curly thin walled unicellular (type 12) trichomes covering the lower leaf surface of *Nothofagus solanderi* (3133), 125 $\times$.

FIGURES 31–36.—31. Scanning electron micrograph of type 12 trichomes showing basal attachment, *Nothofagus solanderi* (3133), 1,000 $\times$.—32. Photomicrograph of type 12 trichomes on the lower surface of a *Nothofagus cliffortioides* (3121) leaf, 250 $\times$.—33. “Thin” walled peltate (type 13) trichomes of *Castanopsis* and *Lithocarpus* spp. (redrawn from Camus 1934–1954, 1948), ca. 200 $\times$.—34. Scanning electron micrograph of type 13 trichomes on the lower foliar surface of *Castanopsis concinna* (3057), 125 $\times$.—35. Photomicrograph of *Castanopsis calathiformis* (3054) showing the characteristic speckled appearance of the lower cuticle produced by type 13 trichome bases, 250 $\times$.—36. Scanning electron micrograph of a rosulate (type 14) trichome on the upper leaf surface of *Quercus arkansana* (610), 500 $\times$.







or, rarely, an intercalary swollen multiseriate section (Figs. 43–45). They are evenly distributed over all orders of venation in young leaves but are often lost with age. In *Quercus* they tend to be more abundant on the upper surface whereas type 15 trichomes are more abundant on the lower. Trichomes of this type are found only in the Quercoideae and Castaneoideae. They reach their maximum development in the genus *Castanea*. Camus (1928–1929) used the term “poil capité” for trichomes of this type. Hardin (1976) called these bulbous trichomes.

Type 17 (large globular). These extremely large trichomes are multicellular and conspicuous. They can be seen with the unaided eye as small dots on the leaf surface (Fig. 46). The component cells are relatively thin-walled, which accounts for the collapse of the structure upon drying (Figs. 47, 48). The stalks are multicellular and leave large scars in the cuticle when lost (Fig. 49). They appear to be glandular in function and may produce the sticky coating characteristic of young *Nothofagus* leaves. These trichomes occur widely scattered over the fine venation on both sides of the leaf. Like most trichomes, they are more abundant on the lower surface, particularly in the tropical species. Large globular trichomes are restricted to *Nothofagus*, in which they can be found in all but a few species.

Type 18 (branched uniseriate). These trichomes are similar to type 15 in cellular composition. They are different from those of type 15 in that they branch at least once (Fig. 50). Branching sometimes results in a nearly equal dichotomy, but more frequently it is irregular and produces a large number of oddly shaped

forms (Figs. 51, 52). The cells are often colored and appear to bear or contain secretory substances. This trichome type intergrades with types 13 and 19. It occurs in the Castaneoideae and Quercoideae, with greatest development occurring in *Lithocarpus*. Trichomes of this type are classified as “simple branched” by Hardin (1976).

Type 19 (“glandular” peltate). These trichomes have cell walls of moderate thickness and a reddish brown glistening appearance. The sheen and color suggest a glandular function although there is no direct evidence to confirm this. This trichome type thoroughly intergrades with type 18 trichomes found on the same leaf (Figs. 51, 53, 54). Type 19 trichomes are found only in *Trigonobalanus doichangensis*. They lack the regularity of type 11 trichomes. This type can be distinguished from type 13 trichomes by its thicker cell walls and darker color. Camus (1934–1954) classified these trichomes as “poils en e’cusson.”

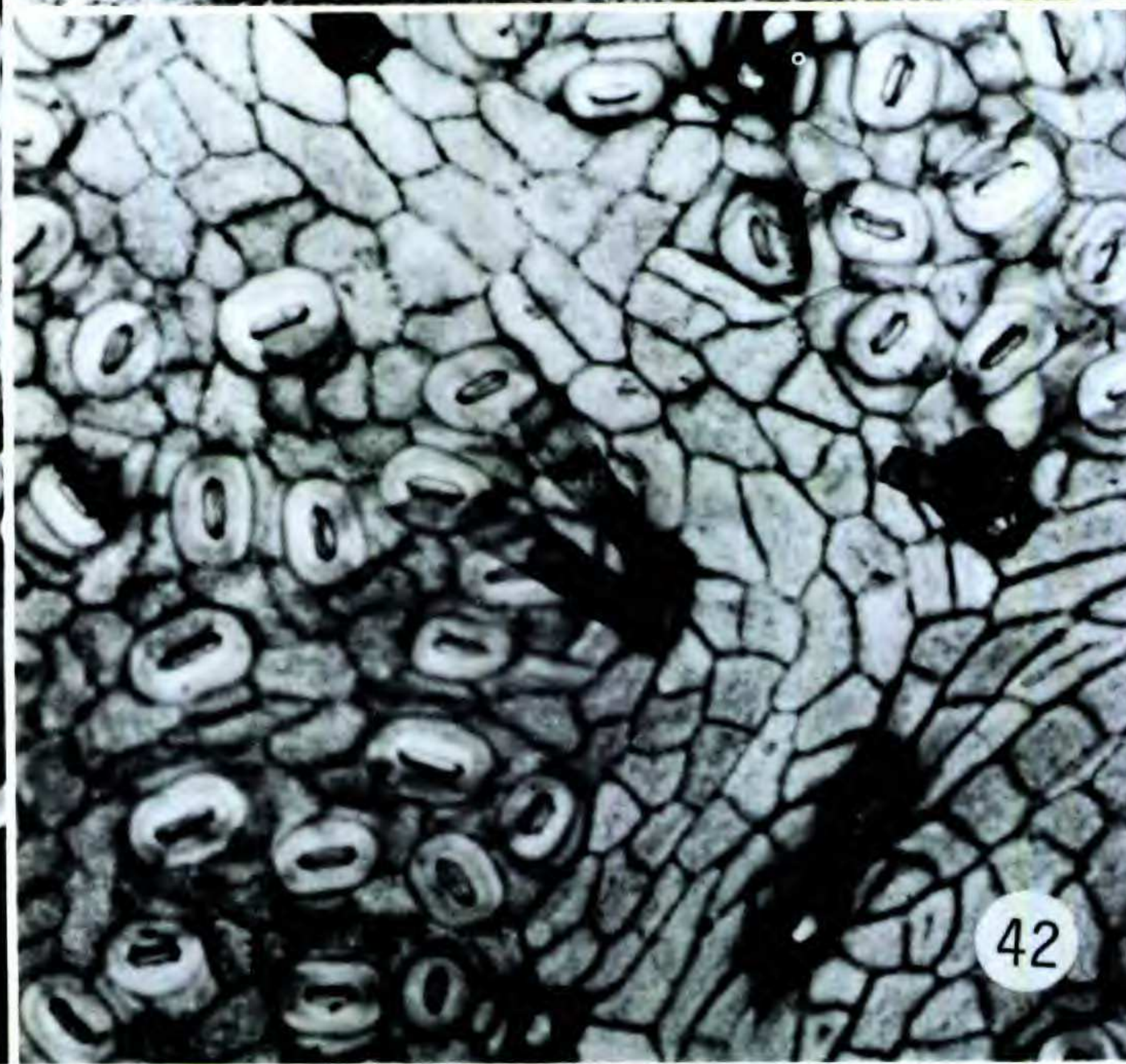
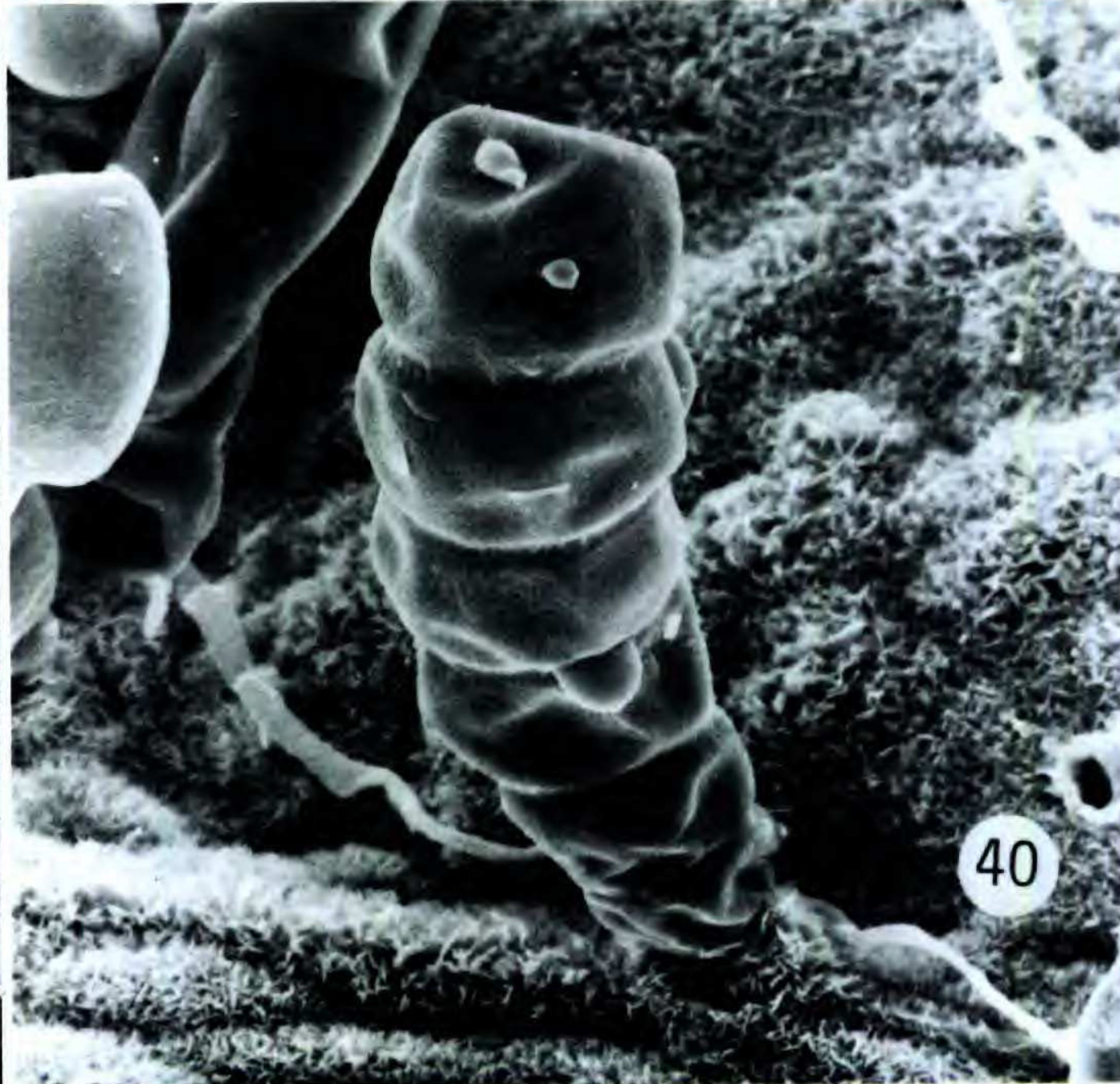
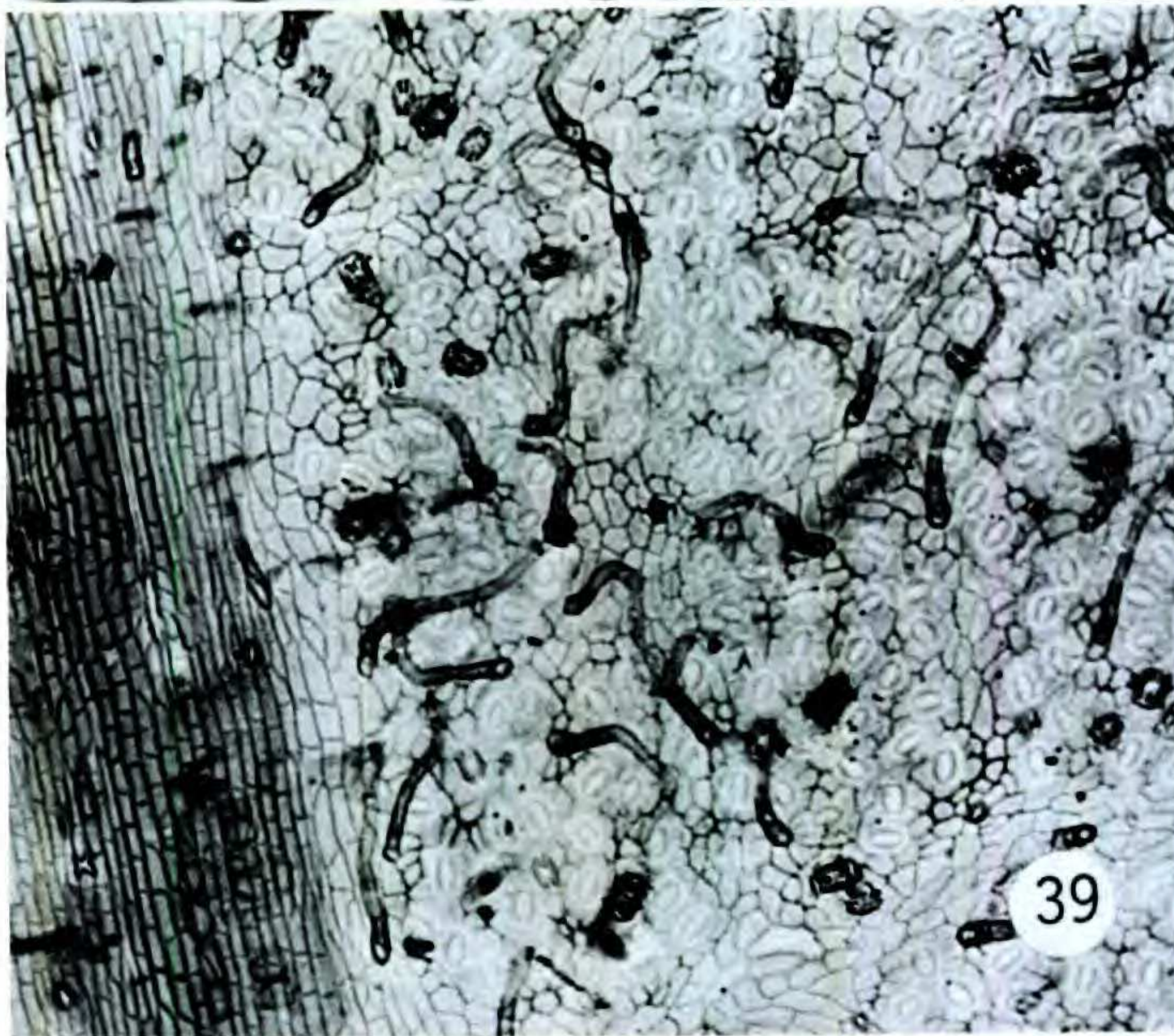
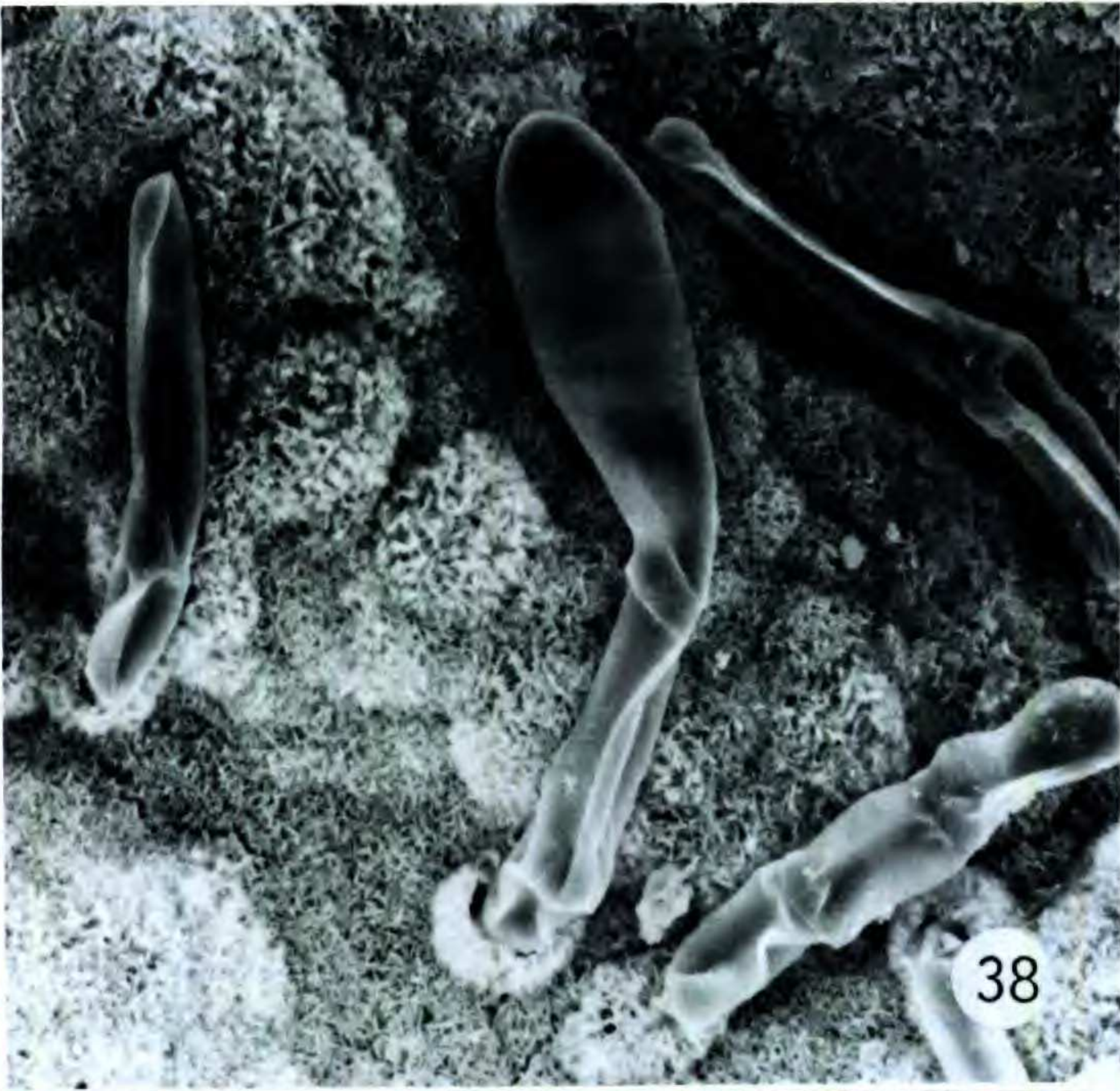
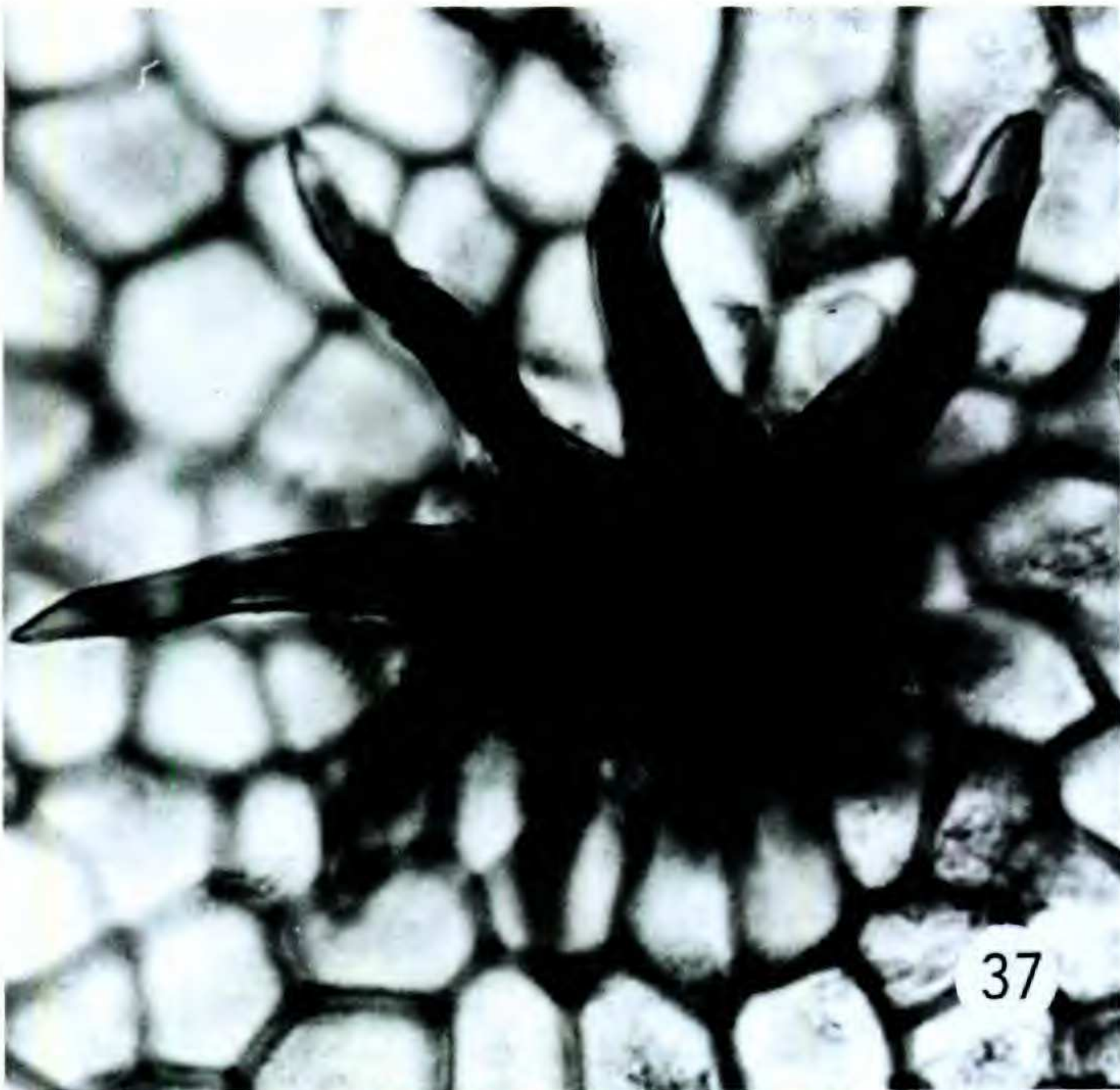
Septate trichomes very similar to those of types 1 and 5 have been reported by Camus (1928–1929, pl. 14:19, 1934–1954, pl. 61:19). The “crosswalls” are not nearly as thick as the side walls. There is no indication of glandular function. In many cases, apparent crosswalls, which may represent the “degenerative membrane thickenings” of Kuester or simply cytoplasmic debris, can be found in unicellular elements. Truly septate trichomes are very rare and have been reported by Camus (1928–1929, 1934–1954) only in the genera *Castanopsis* and *Quercus*. They have also been observed by the author on floral structures of *Chrysopsis*.

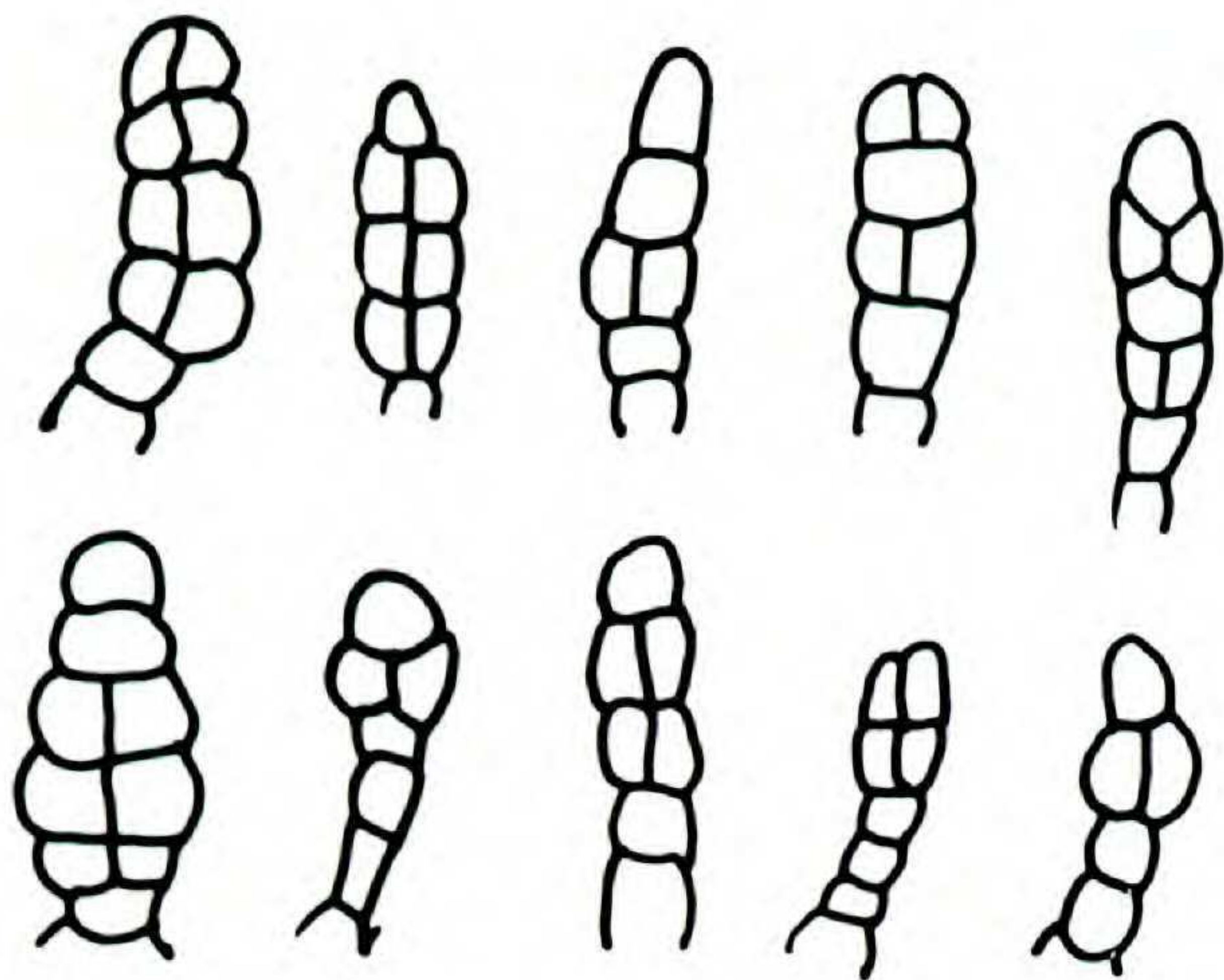
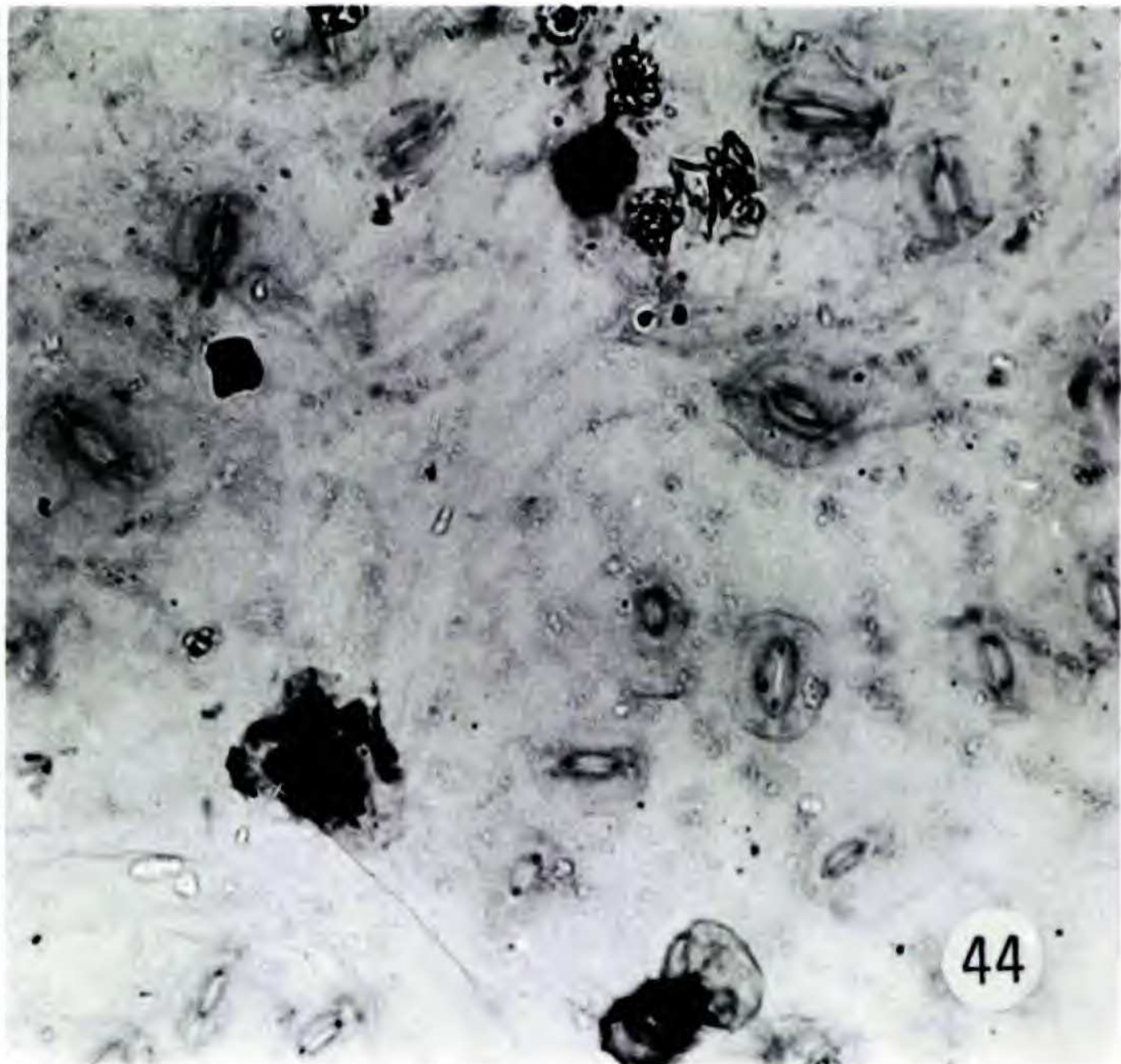
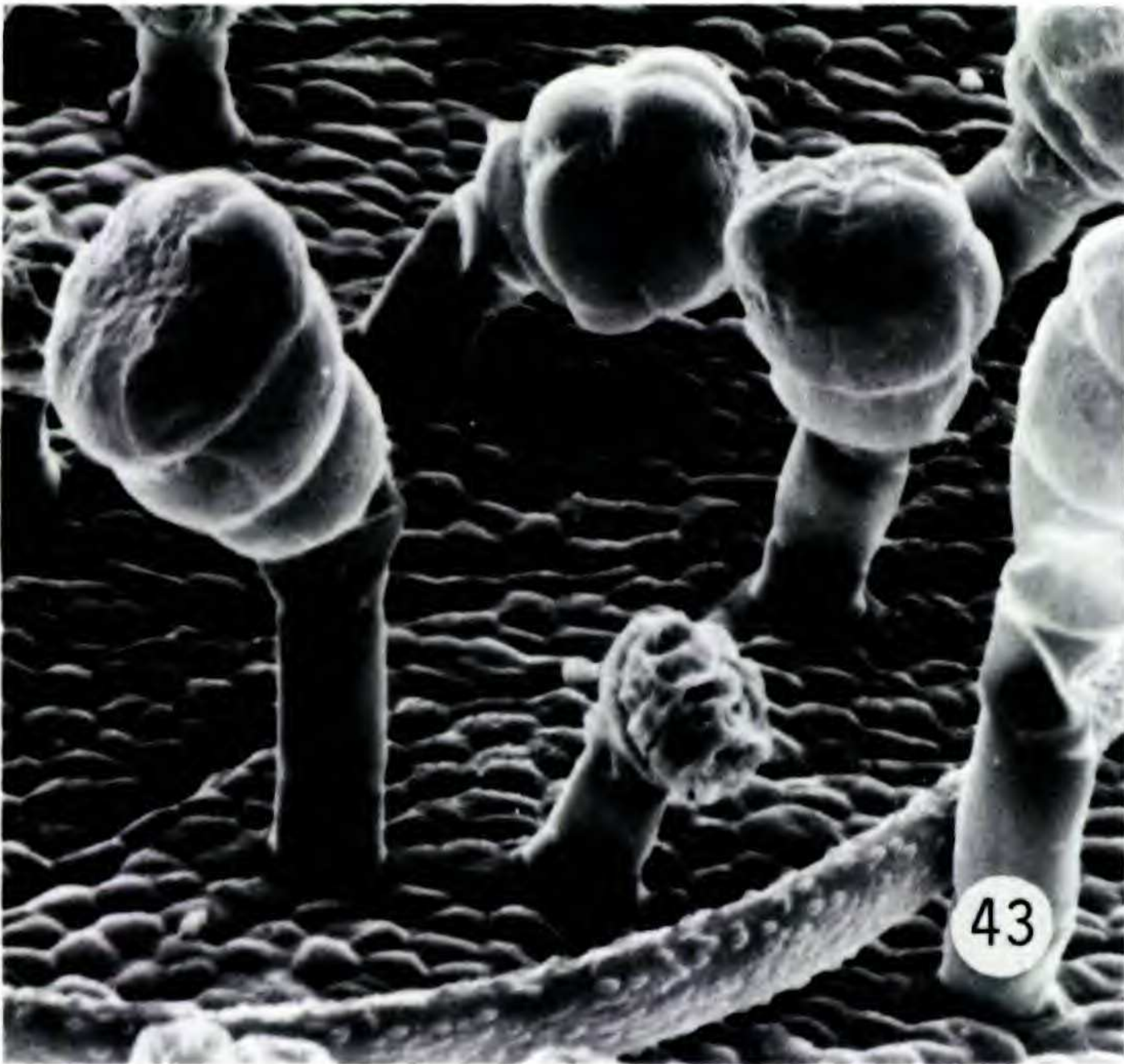
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FIGURES 37–42.—37. Photomicrograph of a type 14 trichome on the upper cuticle of *Lithocarpus cooperta* (3091), 650 $\times$.—38. Scanning electron micrograph of a simple uniseriate (type 15) trichome on the lower leaf surface of *Quercus atriglans* (144), 500 $\times$.—39. Photomicrograph of type 15 trichomes on the lower leaf surface of *Quercus schottkyana* (1186), 250 $\times$.—40. Scanning electron micrograph of a short type 15 trichome composed of spherical cells, lower leaf surface of *Quercus adenonerva* (132), 500 $\times$.—41. Scanning electron micrograph of a long type 15 trichome composed of elongate cylindrical cells, lower surface of a *Quercus acutissima* (1170) leaf, 250 $\times$.—42. Photomicrograph of the resistant basal portions of type 15 trichomes on the lower cuticle of a *Quercus acutissima* (1170) leaf, 250 $\times$.

FIGURES 43–48.—43. Scanning electron micrograph of capitate (type 16) trichomes on the upper surface of a *Castanea crenata* (A1) leaf, 500 $\times$.—44. Photomicrograph of a type 16 trichome from the lower cuticle of *Castanea sativa* (114), 250 $\times$.—45. Drawings of type 16 trichomes, many with intercalary multiseriate sections, *Quercus* spp. (redrawn from Camus, 1934–1954, 1938), ca. 200 $\times$.—46. *Nothofagus bernhardi* (3118) leaf showing large globular (type 17) trichomes scattered over the lower surface, 2 $\times$.—47. Scattered electron micrograph of a collapsed type 17 trichome on the lower surface of a *Nothofagus betuloides* (3119) leaf, 250 $\times$.—48. Scanning electron micrograph of type 17 trichomes scattered among type 2 trichomes on the lower surface of a *Nothofagus antarctica* (3117) leaf, 125 $\times$.

FIGURES 49–54.—49. Photomicrograph of a type 17 trichome base on the lower cuticle of *Nothofagus aequilateralis* (3587), 250 $\times$.—50. Scanning electron micrograph of branched uniseriate trichomes on the lower epidermis of a *Quercus palmeri* (3141) leaf, 125 $\times$.—51. Scanning electron micrograph of type 18 trichomes on the lower epidermis of *Trigonobalanus doichangensis* (1330), 500 $\times$.—51. Drawings of type 18 trichomes from *Quercus* and *Lithocarpus* spp. (redrawn from Camus, 1934–1954, 1948), ca. 100 $\times$.—53. Scanning electron micrograph of a “glandular” peltate (type 19) trichome on the upper epidermis of *Trigonobalanus doichangensis* (1330), 500 $\times$.—54. “Glandular” peltate trichomes of *Trigonobalanus doichangensis* (redrawn from Camus, 1934–1954 and Cutler, 1964), ca. 100 $\times$ (smaller 2) and 160 $\times$ (larger 2).

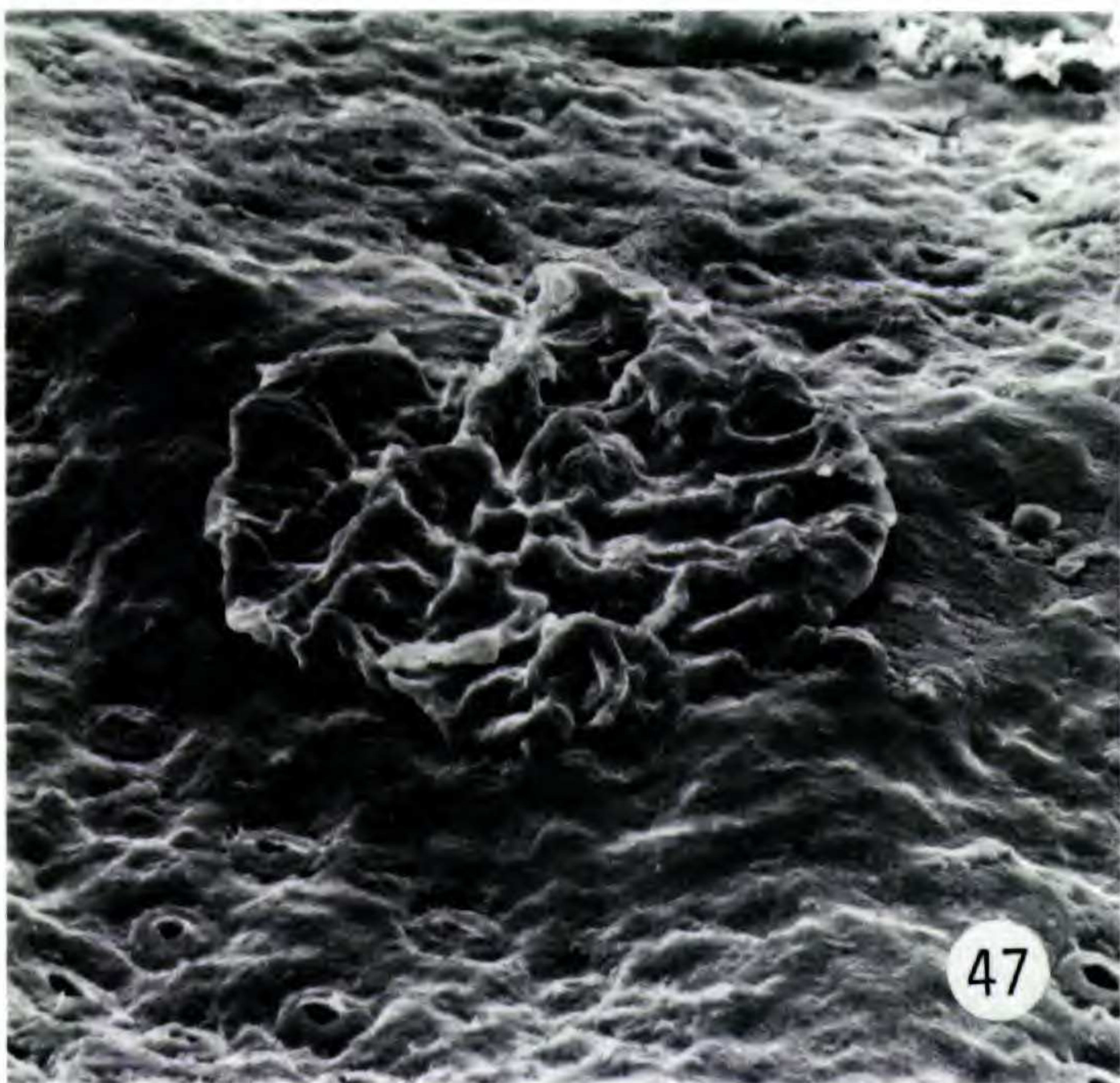




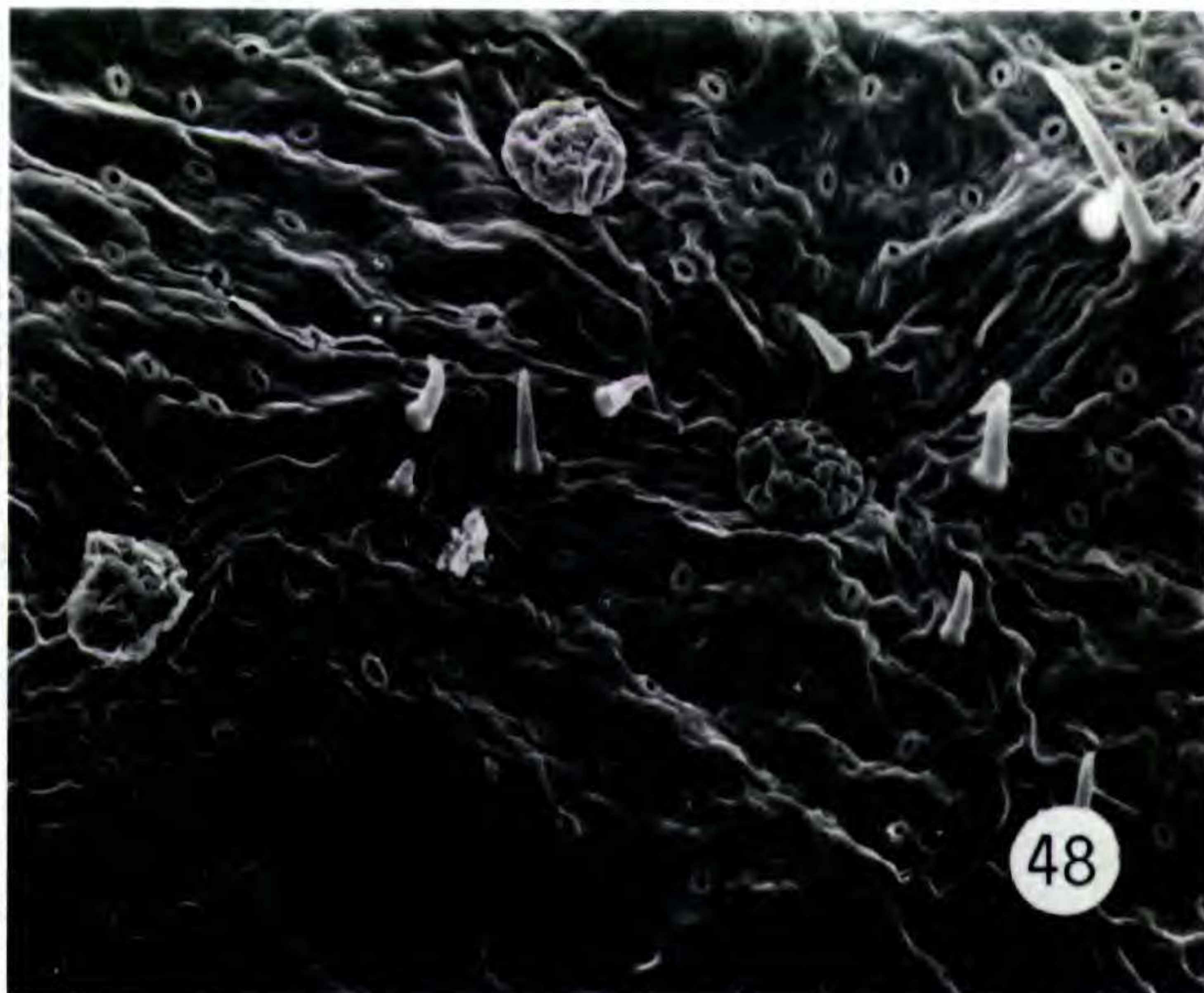
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